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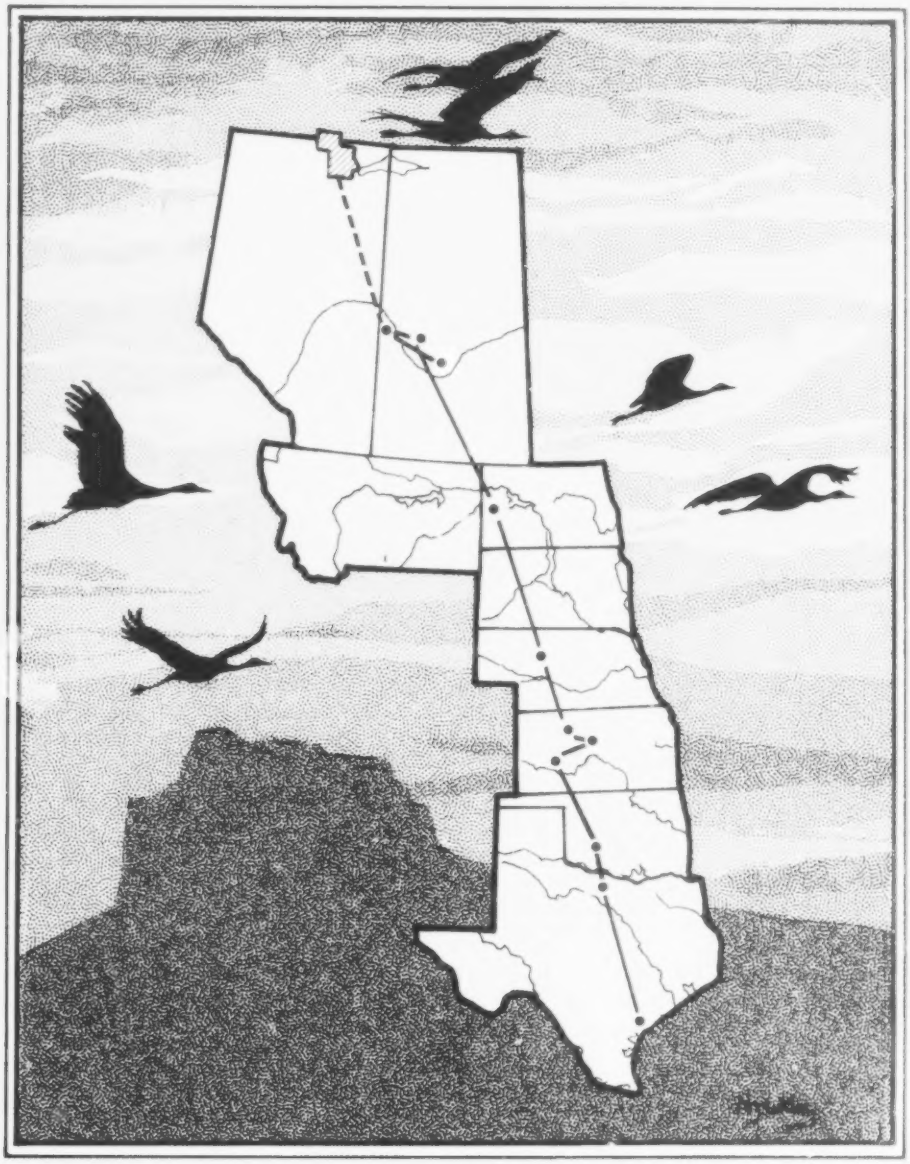
Migration of Radio-marked Whooping Cranes from the Aransas–Wood Buffalo Population: Patterns of Habitat Use, Behavior, and Survival



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By Marshall A. Howe

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Migration of Radio-marked Whooping Cranes from the Aransas–Wood Buffalo Population: Patterns of Habitat Use, Behavior, and Survival

By

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Abstract

Use of migration stopovers by radio-marked whooping cranes (*Grus americana*) between Aransas National Wildlife Refuge, Texas, and central Saskatchewan was studied in fall 1981–83 and spring 1983–84 as part of a cooperative program with the Canadian Wildlife Service. Twenty-seven cranes were monitored for one or several seasons, including nine radio-marked birds and others that associated with them. Whooping cranes showed plasticity in their use of migration habitats, feeding primarily in a variety of croplands and roosting primarily in palustrine wetlands. More than 40% of the roosting wetlands were smaller than 0.5 ha. Although heavily vegetated wetlands were generally not used, family groups appeared to select more heavily vegetated wetlands than nonfamilies. Juveniles allocated 25% more time to foraging than did parents. Parents increased their foraging rate and showed less alert behavior in spring migration. Dissociation of parents and young occurred late in spring migration and after arrival on the breeding grounds. Dancing behavior was most frequent in subadults, suggesting its importance for pair formation.

Although whooping cranes tended to be wary, there was much individual variation in thresholds of tolerance of human activity and disturbance. Hunters were present during large segments of the fall migrations but were not a mortality factor in this study. Of the six deaths of postfledging radio-marked birds, four occurred on the wintering grounds and were attributed to disease (one), predation (one), and unknown causes (two). A juvenile and a subadult died during migration after collisions with power lines. Mortality of postfledging, radio-marked birds was not different from independent estimates of mortality for birds not radio-marked.

Distribution patterns of radio-tracked birds differed greatly from distributions derived from opportunistic sightings. An 85,000 km^2 area in Saskatchewan appears to function as a premigratory staging area in fall. There is no counterpart of the sandhill crane (*G. canadensis*) spring staging area in central Nebraska. Recommendations are suggested for management of whooping cranes during migration.

The remnant population of the endangered whooping crane (*Grus americana*) breeds in Wood Buffalo National Park (WBNP), Northwest Territories and Alberta, Canada, and winters along the Texas coast, primarily on the Aransas National Wildlife Refuge (ANWR). Management of this population has been a priority of the U.S. Fish and Wildlife Service (FWS) and the Canadian Wildlife Service (CWS) for nearly 40 years. Most management efforts have focused on either the breeding or wintering grounds. Before this study was begun in 1981, knowledge of the migration ecology of the species was compiled mostly from anecdotal accounts and incidental observations (Allen 1952; McNulty 1966; Walkinshaw 1973). The rarity of the birds and the relatively short

periods spent at stopovers have impeded detailed studies of migration. In 1977 the FWS accelerated efforts to solicit information on migrating whooping cranes by distributing site evaluation forms to State agencies and individual cooperators for use in describing habitat characteristics of migration stopovers. On the basis of these reports and visits to additional sites, Johnson and Temple (1980) constructed the first profile of the whooping crane's migration habitat.

Analyses of breeding and wintering ground surveys by the Whooping Crane Recovery Team (1980) suggested that a significant proportion of the annual mortality of whooping cranes in the WBNP population might be occurring during migration. They recommended that a study of whooping crane migration be undertaken, employing radiotelemetry as an aid to tracking individuals and groups. Detailed plans for such a study were subsequently developed jointly by FWS and CWS biologists and officials. The objectives of this study were to define migration chronology and routes, describe habitat selection and behavior, and identify hazards and sources of mortality during migration. Here, I summarize data collected by biologists observing the cranes at stopovers located by aerial radio-tracking crews. These data were collected during the fall migrations of 1981–83 and the spring migrations of 1983–84. My role in the study was to organize and coordinate personnel and logistics; to serve as a consultant on data collection methodology; to determine which birds were to be radio-tracked; and to analyze, synthesize, and interpret the data. Kuyt (1987) presented partial results of the 1981 and 1982 migrations. For completeness, I include part of a previous analysis (Howe 1987) of the habitat data from the present study. Because I have reanalyzed some of these data, incorporating additional information, results herein supersede my previous findings (Howe 1987).

Methods

Trapping and Marking

Since 1977, biologists have captured and color-banded prefledging whooping cranes in WBNP as part of a cooperative CWS and FWS program (Kuyt 1979). In July 1981, the first radio-packages, with a life expectancy of 3 years, were applied to bands on three of the prefledging birds, following the procedures of Drewien and Bizeau (1981). In 1982 and 1983, 12 other birds were similarly radio-marked. These 15 radio-marked birds provided options in selecting individuals to be radio-tracked during migration.

Radio-tracking Logistics

Each fall the goal was to radio-track and collect data on two family groups over the entire migratory route—from the Northwest Territories to the Texas coast. Shortly before each of three southward migrations (1981, 1982, 1983), privately contracted amphibious aircraft equipped with standard receiving equipment (Yagi or H antennas and radio receiver) monitored all radio-marked whooping cranes at WBNP. On the departure of a radio-marked chick and its parents on a migratory flight, the pilot and accompanying CWS biologist followed the birds until they reached the prairies of central Saskatchewan. There, after being notified that the birds had departed WBNP, waiting FWS aerial and ground crews assumed radio-tracking responsibilities. The second departing radio-marked crane was similarly followed to central Saskatchewan and turned over to a second team of FWS aerial and ground crews.

In a light aircraft equipped for radio-tracking, each aerial crew, consisting of a pilot and a biologist, followed radio-marked birds during migration flights and reported landing locations to the ground crews. Each ground crew consisted of two biologists with radio-tracking gear and a two-way radio. Their role was to maintain contact with birds on the ground and collect data on habitat use and behavior. A central project coordinator arranged for the personnel, aircraft, and equipment each year and was on call throughout the radio-tracking period to consult, resolve problems, or make critical decisions. Regional coordinators were based in Pierre, South Dakota, and Albuquerque, New Mexico. Besides relaying information between field crews and the central coordinator, regional coordinators were on call to relay crane location information to ground crews if they lost radio contact with aerial crews—a frequent occurrence during long migratory flights.

In a typical sequence after a migratory flight, the aerial crew marked the birds' landing site on a topographic map, then landed at the nearest air strip and called the regional coordinator with the information and a number where they could be reached. After the ground crew obtained the information, they proceeded to the approximate landing site, listened for the radio signal and, if successful, made visual contact. They remained with the cranes until dark and then sought hotel accommodations. On clear nights with northerly winds, they often made a late-night check for the radio signal in case the birds moved after dark. If the birds had not moved, the crew located them at dawn and collected data on behavior and habitat throughout the day. If the birds had resumed migration, the ground crew notified the aerial crew, who resumed radio-tracking, keeping radio contact with the ground crew as long as possible.

Except for rare instances in which biologists lost contact with the cranes, this procedure worked efficiently and became routine.

Crews followed similar procedures during spring radio-trackings (1983 and 1984) except that they were able to rendezvous in advance at ANWR, the point of departure. Ground crews could continue only as far as the roadless, forested area of central Saskatchewan. The aerial crews continued to follow the cranes from that point toward WBNP. Complete surveillance was not usually possible, however, because float planes could not be used in spring. When aerial crews lost track of birds in this area, they continued on to WBNP and tried to locate them soon after their arrival. We occasionally contracted with a commercial flight service in Fort Smith, Northwest Territories, for the same purpose. Canadian Wildlife Service biologists periodically checked on radio-marked birds in the course of summer breeding studies.

Choice of individuals to track was a compromise between two conflicting objectives: to determine if particular individuals used the same stopovers traditionally in different years and to maximize the number of individuals tracked (thereby reducing statistical bias). We attempted to address both objectives by (1) selecting one individual to follow through every migration and by (2) selecting an individual not previously radio-tracked as the other target in each migration. Because the pool of radio-marked birds increased each year, the second objective became easier to meet later in the study. In practice, the first aerial and ground crews always followed the first departing bird. If that bird happened to be the target individual for study of traditionality, the second crews followed a bird not previously radio-tracked. Otherwise, the second crews followed the target individual regardless of other radio-marked birds departing in the meantime.

Data Collection

My paper concerns data collected by the ground crews. Ground crews described the habitats used for feeding, roosting, and resting at migration stopovers and developed behavioral profiles of the birds. Each crew also maintained a chronological journal of the birds' daily movements and other information considered important. These journals provided the basis for narrative summary reports prepared at the end of each migration. The field biologists submitted the reports and data forms to the central coordinator, who compiled and analyzed them.

Habitat Characterization

Ground crews completed a coded form for each feeding, roosting (overnight), and resting site (a daytime site used by cranes for resting or drinking between feeding bouts). If a site served more than one function, it was included in the data sets for each.

Crews assigned habitat to one of six wetland or two upland categories. Wetlands were classified according to the Cowardin et al. (1979) definitions of wetland systems and wetland system modifiers. Density and distribution of emergent vegetation were assessed visually and assigned to one of five categories. Biologists either measured water depth at locations where cranes roosted or fed, or estimated depth from the submerged portion of the leg. Slope of the land and horizontal visibility from crane head height in four compass directions from each site were estimated and averaged. From topographic maps and general knowledge of the local area, ground crews also estimated the availability of similar sites within a 16-km radius of each roosting wetland. Estimates were assigned to one of four subjective categories ranging from none to abundant. Additional variables for which data were collected included substrate texture in wetlands (sand, hard mud, soft mud); water turbidity (high, medium, low); dominant vegetation (taxon); land ownership (private, Federal, regional government); and estimated future security of the site (stable, threatened, unknown). Some observers recorded the distance from roosting or feeding sites to the nearest road or habitation. Landowners were interviewed to ascertain whether the sites used by cranes would be subject to modification in the foreseeable future. Observers also recorded the legal description of the site, using the township-range system, and they photographed each site.

Behavior

Ground crews collected time-activity budget data during each migration after 1981. Although they attempted two complete 2-h observations daily, movement of the birds often resulted in abbreviated observation periods. One observer monitored the stopwatch and recorded and coded instantaneous behavior data described by the other observer at 30-s intervals. To obtain information on diurnal variation, data were collected in both early morning and midafternoon when possible. Because of these recommended times, ground crews collected few data on activities at roosting wetlands. One of the crews (Ward 1984) attempted to distribute activity data collection evenly throughout daylight to better define diurnal activity patterns. Smith (1983) determined general diurnal activity patterns (e.g., feeding, flying, resting) by translating field notes into timelines of activity between dawn and dusk for four groups of fall migrants in 1982.

Table 1. *Identification data and radio-tracking histories of target radio-marked whooping cranes.*

FWS band number	Color band combination[a]	Nest number/ hatching year	Season and year tracked	Comments[b]
629-01807	W-R/W	7/81	Fall 1981	Migrated with two parents. Tracked to ANWR.
			Fall 1982 (part)	Associated in Saskatchewan with three adults, including R-R and R-R/W. Not tracked south of Canada. Found dead near Waco, Texas, 16 October 1982.
629-01808	R/W-G	2/81	Fall 1981	Migrated with two parents. Struck power line near Glaslyn, Saskatchewan, 11 October and died in captivity 18 October 1981.
629-01810	W-R	10/82	Fall 1982	Migrated with two parents. Tracked to ANWR.
			Spring 1983	Migrated with two parents. Tracked to Meadow Lake, Saskatchewan. Departed Meadow Lake after 1 May. Parents found at WBNP on 9 May. W-R found 28 May, 17 km south of parental territory.
			Fall 1983	Migrated with yearling G-W/R (nest 2/82). Tracked to ANWR.
			Spring 1984	Migrated again with G-W/R. Tracked to WBNP, arriving 22 May.
629-01811	W/R-G	1/82	Fall 1982 (part)	Migrated with two parents. Another pair joined them. After injury to one parent, tracking discontinued in Saskatchewan, 24 October. Observed again 27 October. W/R-G found dead at ANWR, 2 February 1983.
629-01815	B/W-R	6/82	Fall 1982 (part)	Migrated with two parents. Monitored by ground crews from 24 October in Saskatchewan to ANWR. Found dead on Matagorda Island, ANWR, 4 January 1983.
629-01812	G-W/R	2/82	Spring 1983	Migrated with two parents. Tracked to WBNP, arriving 22 April. Family group intact on parental territory 23 April. G-W/R found alone about 17 km away on 3 May.
			Fall 1983	Migrated with yearling W-R (nest 10/82). Tracked to ANWR.
			Spring 1984	Migrated again with W-R. Tracked to WBNP, arriving 22 May. Found dead at ANWR, 15 November 1984.
599-09822	R-Y	19/83[c]	Fall 1983	Migrated with two parents. Joined by two other whooping cranes in Saskatchewan and a third in North Dakota. Tracking discontinued in Oklahoma. Birds located the next day in Matagorda Bay, Texas. Believed to have flown nonstop from Pierre, South Dakota, to the Gulf of Mexico.
			Spring 1984	Migrated with two parents and up to four others, including radio-tagged G-R/W (nest 3/81). Parents and R-Y separated in Saskatchewan on 26 April. R-Y remained in Saskatchewan until about 9 May and was located in WBNP on 17 May.

[a]Colors: white, red, green, blue, yellow. Combination order: upper/lower left leg-upper/lower right leg.
[b]ANWR = Aransas National Wildlife Refuge (Texas); WBNP = Wood Buffalo National Park (Canada).
[c]Mistakenly referred to as nest 14/83 in Ward (1984). Determined to be 19/83 on the basis of winter territory occupancy (Stehn 1984).

Data Analysis

The habitat use and activity budget forms contained all quantitative data analyzed in this report. I examined all data forms for obvious errors or omissions. Most problems I corrected by contacting the observer or by comparing the data with summaries in the interim narrative reports. The data were then keypunched onto computer tape for summary and analysis—the Statistical Analysis System (Ray 1982) was used for statistical analyses.

I summarized categorical habitat data in a series of frequency distribution histograms, making each bar represent the number of roosting or feeding sites in that category, unweighted by the time birds spent at the site. Most figures present histograms of two subsets of the data for that variable (e.g., spring and fall, adults and juveniles). I tested the null hypothesis that the distributions for each subset were identical, by using the chi-square (χ^2) goodness-of-fit test. Although I assumed for all analyses that the data points were independent, the data were in fact based on a small number of individuals sampled repeatedly—thus, the assumption of independence was necessarily violated. However, it is likely that individual differences were generally minor at these coarse-grained levels of analysis, compared with differences between adults and juveniles or other groupings examined in this study. Nonetheless, I used analysis of variance (ANOVA), incorporating individual identity as a covariable, for analyzing data subsets involving small numbers of individuals. I did not conduct chi-square tests when any expected value was below 0.5 or when two were below 1.0 (Steel and Torrie 1980).

Results

Radio-tracking Histories and Geographic Distribution

Data were collected on 27 whooping cranes—including detailed information on 7 radio-marked birds (Table 1)—during fall migrations in 1981–83 and spring migrations in 1983–84. The degree to which field crews monitored these individuals varied from a few days to four nearly complete migrations (in the case of bird W-R).

Whooping cranes departed WBNP on northerly winds between mid-September (nonbreeders) and mid-October (some family groups). Birds traveled alone, as family groups, or in small groups (e.g., three to five) of unrelated individuals. In about 2 days they arrived in the central Saskatchewan prairies, where they remained for a typical period of several weeks (Kuyt 1987), feeding primarily on grain crops and roosting in wetlands. Within the Saskatchewan prairie system movement patterns were variable, but most individuals confined activities to a local area until active migration resumed. The remainder of the migration to ANWR was rapid (5–15 days), involving daily migration flights when winds were favorable. Patterns of habitat use at stopovers were similar to those in Canada, except that feeding bouts were brief or nonexistent on days of lengthy flights. In spring, birds departed ANWR on southerly winds between late March (breeders) and mid-April (usually nonbreeders). Juveniles from the previous year migrated with their parents as far as the Saskatchewan prairies or to WBNP.

Although the number of migration stopovers was distributed broadly among the States and Saskatchewan (Fig. 1), more than 43% of crane use-days were in Saskatchewan, particularly in fall (Table 2). Kansas and Nebraska were the most heavily used States in spring.

Fig. 1. Composite of migration roosting stopovers (north to edge of inaccessible forest) used by radio-tracked whooping cranes during the present study. Multiple sites used by one crane group spending several days in a local area are shown as one site.

Table 2. *Geographic distribution of stopovers[a] and use-days[b] of radio-marked whooping cranes in spring, fall, and both seasons combined, 1982–84.*[c]

Area	Spring		Fall		Combined	
	Number (%) of stop-overs	Number (%) of crane use-days	Number (%) of stop-overs	Number (%) of crane use-days	Number (%) of stop-overs	Number (%) of crane use-days
Texas	4 (10.3)	26 (8.6)	8 (17.0)	27 (9.5)	12 (14.0)	53 (9.0)
Oklahoma	2 (5.1)	5 (1.6)	6 (12.8)	23 (8.1)	8 (9.3)	28 (4.8)
Kansas	10 (25.6)	62 (20.4)	2 (4.3)	5 (1.8)	12 (14.0)	67 (11.4)
Nebraska	12 (30.8)	57 (18.8)[d]	3 (6.4)	9 (3.2)	15 (17.4)	63 (10.8)
South Dakota	2 (5.1)	6 (2.0)	6 (12.8)	14 (4.9)	8 (9.3)	20 (3.4)
North Dakota	4 (10.3)	15 (4.9)	2 (4.3)	6 (2.1)	6 (7.0)	21 (3.6)
Montana	0 (0)	0 (0)	1 (2.1)	6 (2.1)	1 (1.2)	6 (1.0)
Saskatchewan	5 (12.8)	133 (43.7)	19 (40.4)	195 (68.4)	24 (27.9)	328 (56.0)

[a]Wetlands in close proximity used by a particular group of birds in a particular migration are treated as one stopover.
[b]Defined as one crane using a stopover for 1 day.
[c]Table does not include crane groups for which only partial data were available for a given migration.
[d]Forty-two of the 57 are attributable to 2 subadults that spent 3 weeks in Nebraska in 1984.

Oklahoma and Texas in fall. No radio-marked crane used any specific site during different migrations, and separate radio-marked birds never used the same site either within or among migrations. However, several general areas were used by more than one radio-tracked group. The general locations with the most duplication of use were Byers Lake, Texas; Williston, North Dakota; and Glaslyn, Saskatchewan.

Habitat Use

General Habitat Use Patterns

The frequency distributions of roosting sites and feeding sites among general habitat categories (Fig. 2A; Tables A1 and A2) differed greatly ($\chi^2 = 45.5$, $P = 0.0001$). With one exception, all roost sites were wetlands. The remaining site was a sand dune adjacent to muskeg in Alberta. In contrast, 42% of feeding sites were croplands, primarily wheat and barley stubble in Canada and wheat and milo stubble in the United States. Recently swathed but unharvested fields were also used. Because many feeding sites were actually roosting sites in which occasional feeding took place, a time-weighted analysis of feeding would probably show croplands to be more important than the 42% value suggests.

Cranes roosted in natural ponds and lakes more often in fall than in spring, when transitory wetland types received heavier use (Fig. 2B; $\chi^2 = 13.4$, $P = 0.04$). Feeding habitats did not differ in spring and fall with respect to wetland type ($\chi^2 = 6.8$, $P = 0.44$). Ponds and lakes were more frequently used for roosting by nonfamilies than by family groups (Fig. 2C; $\chi^2 = 17.0$, $P = 0.009$). Family groups showed a broader roosting distribution among wetland types, making greater use of wetlands that generally were shallow throughout. Croplands composed 70% of the feeding sites used by nonfamilies, while 67% of the feeding sites used by families were wetlands (Fig. 2D).

Wetland System and System Modifiers

Most roosting sites and feeding wetlands were palustrine (Cowardin et al. 1979; Fig. 3A). Although family groups and nonfamilies roosted in similar wetland systems, families may have favored palustrine wetlands for feeding more than nonfamilies (Fig. 3B; expected values too small for analysis). Feeding and roosting sites were similarly distributed according to wetland modifiers (Cowardin et al. 1979; Fig. 4A; $\chi^2 = 3.9$, $P = 0.56$). The cranes used intermittently exposed and semipermanent wetlands more than any other type. Although they used temporary wetlands extensively for roosting in spring, they more often used intermittently exposed wetlands in fall (Fig. 4B; $\chi^2 = 15.3$, $P = 0.003$). A similar pattern prevailed in feeding wetlands. Families and nonfamilies showed similar distributions with respect to roosting wetland modifier categories ($\chi^2 = 8.1$, $P = 0.09$) and probably also with respect to feeding wetland modifier categories (expected values too small for analysis).

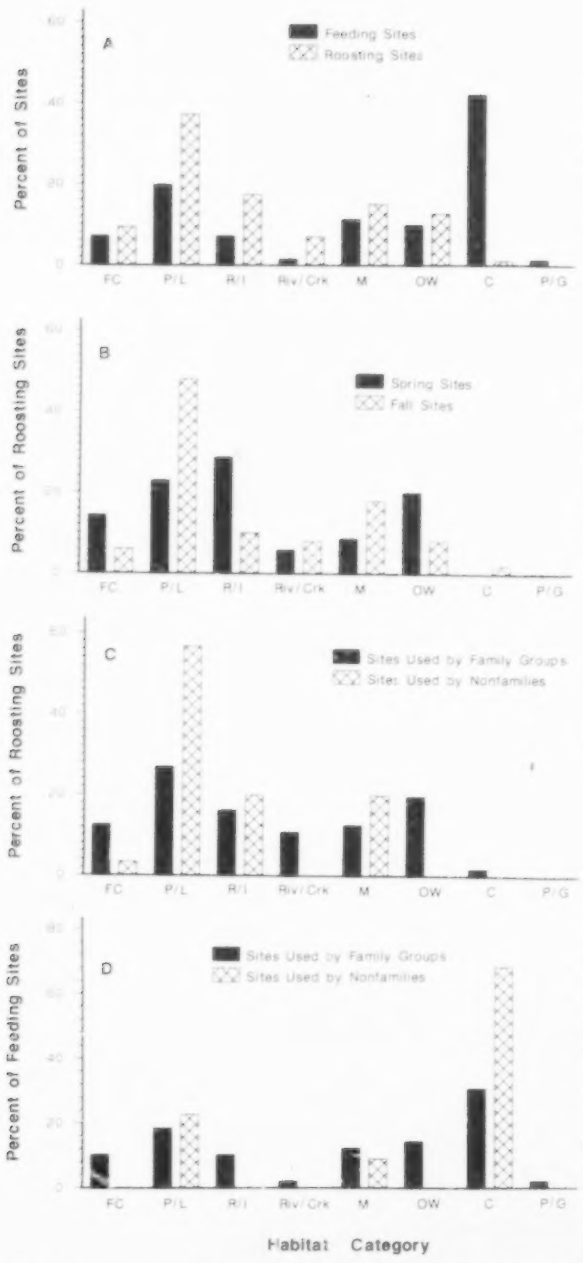

Fig. 2. Frequency distributions of habitat use by whooping cranes for: (A) feeding (N = 71) and roosting (N = 86) sites; (B) spring (N = 35) and fall (N = 50) roosting sites; (C) family (N = 56) and nonfamily (N = 30) roosting sites; (D) family (N = 49) and nonfamily (N = 22) feeding sites. Habitats are: FC = flooded cropland; P/L = pond/lake; R/I = reservoir/impoundment; Riv/Crk = river/creek; M = marsh; OW = other wetland; C = cropland; P/G = pasture/grassland.

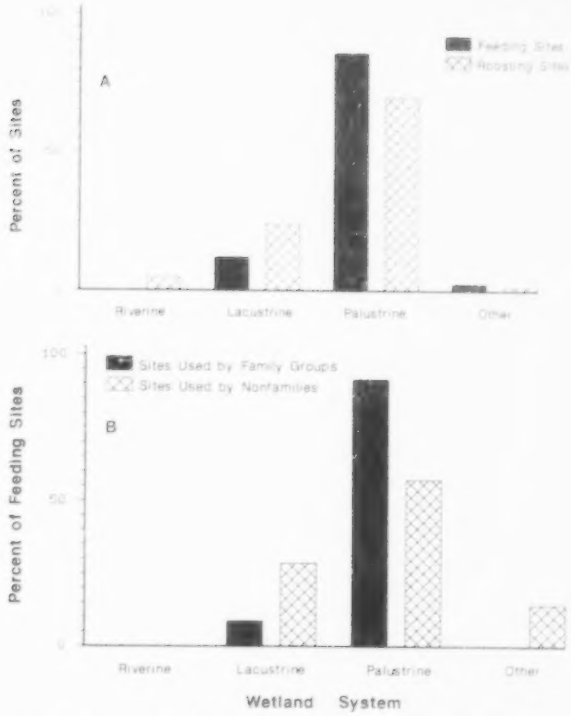

Fig. 3. Frequency distributions of wetland system (Cowardin et al. 1979) use by whooping cranes for: (A) feeding (N = 42) and roosting (N = 83) sites; (B) family (N = 35) and nonfamily (N = 7) feeding sites.

Vegetation Density

The cranes rarely used densely vegetated wetlands. Ground crews described most sites as having scattered vegetation (Fig. 5A). There was a slight (χ^2 = 8.9, P = 0.06) indication that the birds used wetlands with no vegetation or with a perimeter of vegetation more often as roosting sites than as feeding sites, which tended to have scattered or clumped vegetation. Family groups roosted in wetlands with clumped vegetation more often than nonfamilies, but nonfamilies roosted more commonly in wetlands with peripheral vegetation (Fig. 5B; χ^2 = 10.7, P = 0.03). One crew member reported that dense emergents were used during high wind; Lewis (1976) reported similar behavior for sandhill cranes.

Miscellaneous Variables

Generally, cranes did not venture into water deep enough to cover the hock (tibiotarsal-tarsometatarsal joint). Water depth measurements averaged 14.1 cm (SD = 9.0 cm, N = 78) in roosting wetlands and 20.2 cm

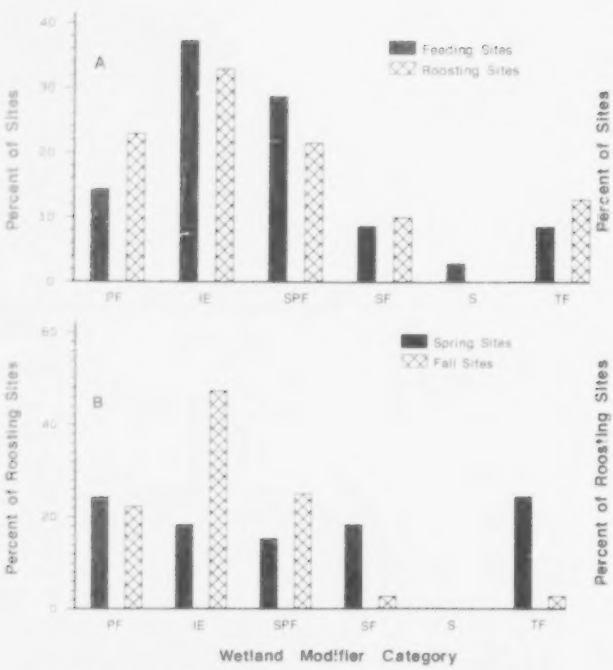

Fig. 4. Frequency distributions of wetland system modifier (Cowardin et al. 1979) use by whooping cranes for: (A) feeding (N = 35) and roosting (N = 70) sites; (B) spring (N = 33) and fall (N = 36) roosting sites. Modifiers, in decreasing order of water permanence, are: PF = permanently flooded; IE = intermittently exposed; SPF = semipermanently flooded; SF = seasonally flooded; S = saturated; TF = temporarily flooded.

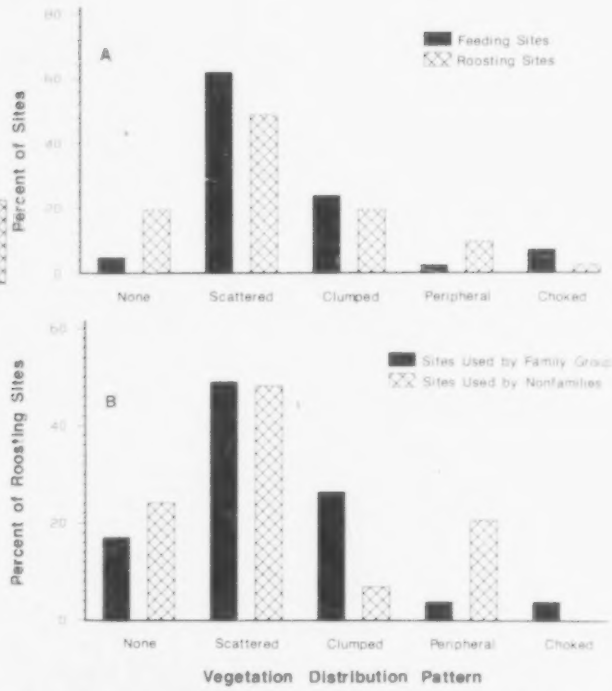

Fig. 5. Frequency distributions of use of vegetation distribution categories by whooping cranes for: (A) feeding (N = 42) and roosting (N = 82) wetlands; (B) family (N = 53) and nonfamily (N = 29) roosting wetlands. Category definitions are: None = no emergent vegetation; Scattered = distributed irregularly in no definable pattern and in low enough density that water is clearly visible; Clumped = distributed in discrete patches with open water between; Peripheral = distributed around the perimeter of the wetland with open water in the middle; Choked = distributed throughout at a density high enough that water is not clearly visible.

(SD = 38.9, N = 39) in feeding wetlands. Water turbidity was not a factor in wetland selection. Although most roosting and feeding wetlands had clear water (i.e., bottom visible), many also showed varying degrees of turbidity (Fig. 6). Similarly, there was no evidence of selection on the basis of substrate texture (Fig. 7). Although cranes rarely roosted in steep-sided wetlands (mean slope estimate of surrounding land, 7.1°), the birds did not appear to select sites with relatively unlimited visibility (Table 3). Sixty-four percent of roosting sites had a maximum visibility of less than 2 km; visibility was less than 1 km at 16.5% of sites.

Cranes observed in this study used a wide range of wetland sizes, including some of the smallest natural wetlands and stock ponds (Table 4). Of the 69 roosting wetlands for which ground crews made area estimates, 15% were smaller than 0.1 ha and nearly 41% were smaller than 0.6 ha. The range of wetland sizes used was

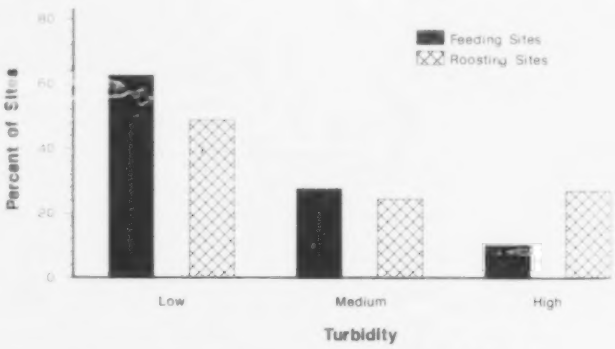

Fig. 6. Frequency distributions of whooping crane feeding (N = 40) and roosting (N = 82) wetlands among categories of turbidity.

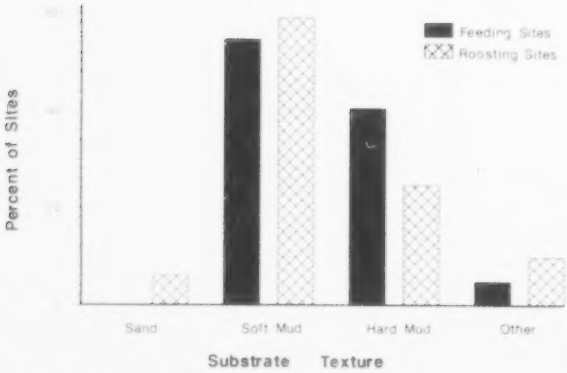

Fig. 7. Frequency distributions of whooping crane feeding (N = 42) and roosting (N = 81) wetlands among categories of substrate texture.

most limited in Nebraska, where the largest was only 8.8 ha.

Feeding and roosting sites were typically (56%, N = 73) less than 1 km apart, but occasionally (14%) were separated by more than 8 km (Table 5). Eighty-four percent of the roosting sites in Canada and the United States had abundant or moderate amounts of similar habitat within a 16-km radius. These estimates, however, were based on general observations and examination of topographic maps by ground crews, not on detailed examination of alternative sites. Of all feeding and roosting sites, 75–80% were on private land (Fig. 8). The remainder were in other land ownership categories, including Federal and State land. Interviews with landowners suggested that more than 80% of the sites were secure for the future—only 5% were considered threatened. There were no significant differences between feeding and roosting sites in their apparent short-term security (χ^2 = 2.3, P = 0.32).

Behavior and Time Allocation

General Behavior Patterns

All birds exhibited generally predictable diurnal activity at migration stopovers, except on days of migration flights. After roosting for the night in a wetland, the birds either walked or flew to nearby cropland around sunrise and began to forage. Periodically they interrupted bouts of feeding with resting, during which they preened, drank, and slept. Birds either returned to the roosting wetland to rest or rested in a shallow wetland, such as a flooded portion of the cropland within walking distance or a short flight from the principal feeding area. Members of family groups in particular often fed at the resting site on waste grain or aquatic vertebrates and invertebrates. Several different feeding sites were often used in the same day. In an analysis of one fall family group (Ward 1984), birds averaged five feeding bouts per day, with total feeding time divided evenly between morning and afternoon and separated by resting periods. Feeding was least frequent during the hour before noon. Relative amounts of time spent feeding and resting varied from day to day and among crane groups.

The initiation time and duration of migration flights were dependent in part on favorable weather but were highly variable even on days with seemingly optimal weather conditions. Some flights began near dawn, some in midmorning, and some in the afternoon. Because of this variability, there were no clear patterns of habitat use before, after, or between flights. Although ground crews seldom kept complete dawn-to-dusk records of the habitats occupied by the cranes, I attempted to reconstruct this information from field journals. Timeline data for the crane family with the most complete coverage (family 10/82, fall 1982; Smith 1983) showed considerable day-to-day variation in sequence and duration of activities (Fig. 9).

Table 3. *Frequency distributions of maximum and minimum horizontal visibility[a] distances from roost sites used by radio-marked whooping cranes, spring and fall 1982–84.*

	Maximum visibility		Minimum visibility	
Distance category (km)	Number of sites	Percent of sites	Number of sites	Percent of sites
<1	16	16.5	78	80.4
1–2	46	47.4	16	16.5
2–5	16	16.5	1	1.0
>5	20	19.6	2	2.1

[a]Measured from crane head level.

Table 4. *Areas (ha) of wetlands used as roosting sites by radio-marked whooping cranes, spring and fall 1982–84.*

Area class (ha)	Frequency	Percent
<0.1	10	14.5
0.1–0.5	18	26.1
0.5–1.0	8	11.6
1.0–6.0	11	15.9
6.0–11.0	4	5.8
11.0–20.0	2	2.9
20.0–100.0	3	4.3
100–1000	6	8.7
>1000	7	10.1

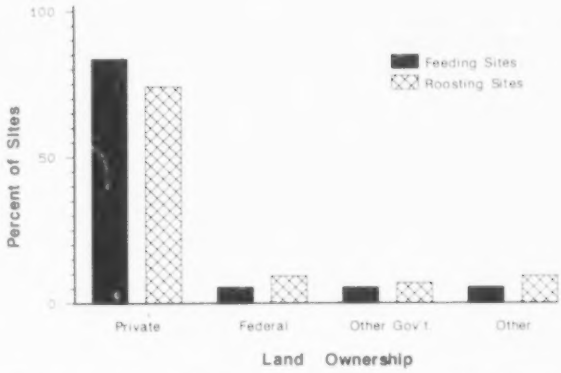

Fig. 8. Frequency distributions of whooping crane feeding (N = 73) and roosting (N = 85) sites among categories of land ownership.

Variability in time allocated to various activities also appeared to be high among groups of cranes (Table 6).

Although sample sizes for both crane groups and days with adequate data are small, the timelines indicate that the cranes spent proportionally more time feeding in fall than in spring (Table 6). When Canadian and United States portions of fall migration are compared, a tradeoff between time spent feeding and flying is evident. The United States segment is typified by long flights and short feeding bouts; the Canadian segment is a more leisurely period of feeding and resting in preparation for the accelerated migration to follow.

Time-activity Budgets

Summaries of time allocation to each of 10 behaviors, based on instantaneous sampling, show that feeding was by far the most frequent behavior (41.1% of the time), followed by standing, walking, preening, and alert behavior (Table 7). Analysis of variance that used individual identity as a covariable did not reveal statistical differences in frequencies of occurrence of behaviors among the six subsets of the data examined, perhaps because of the small number of individuals observed. One apparent difference was the high incidence (21.9%) of alert behavior shown by parent birds during fall migration, followed by a decline to 4.6% during the return migration in spring. Agonistic behavior, although infrequent, also declined sharply from fall to spring. Juveniles exhibited a high incidence of foraging in their first fall and spring migrations. Both spring and fall values for juveniles were substantially higher than those for parents or the combined mean for all birds. Parent birds showed a slight increase in foraging incidence from fall to spring, while subadults showed the opposite pattern. Dancing behavior, though occurring almost any time in any age class, was least frequent in both fall and spring juveniles, intermediate in parents and in fall nonbreeders, and most frequent in spring subadults.

The sampling effort for activity was unevenly distributed throughout daylight (Fig. 10). Therefore these results (Table 7), which are time-weighted by 2-h observation blocks, are biased toward the 0800–1000-h period and away from the 1200–1400-h and 1800–2000-h periods. However, as there was no striking periodicity in diurnal behavior, it is unlikely that the activity summaries are seriously distorted by the distribution of observer effort. For example, foraging frequency showed only minor fluctuations in the 35–45% range throughout the day until the 1800–2000-h period, when it decreased to 30% (Fig. 11). The minor variation observed was compensated by increases or decreases in behaviors associated with resting. Because distribution of observer effort was comparable

Table 5. *Distances (km) between corresponding roosting and feeding sites used by radio-marked whooping cranes in spring and fall 1982–84.*

Distance class (km)	Frequency	Percent
<0.1	12	16.4
0.1–0.5	11	15.1
0.5–1.0	18	24.7
1.0–3.0	9	12.3
3.0–5.0	9	12.3
5.0–8.0	4	5.5
>8.0	10	13.7

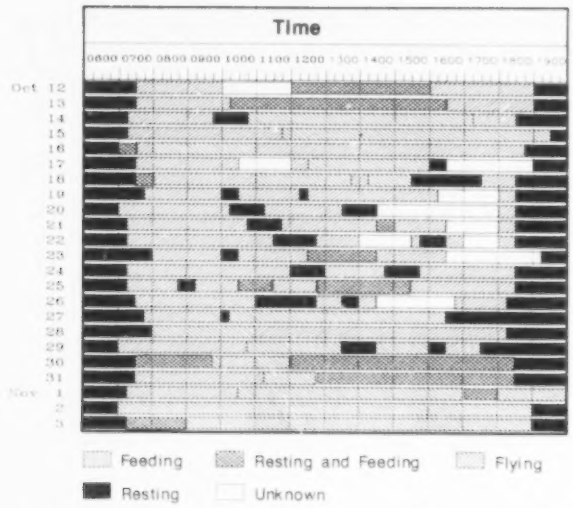

Fig. 9. Timelines of general daily activity of whooping crane family 10/82 during the fall 1982 migration (adapted from Smith 1983).

among the six categories of birds analyzed (Table 7), comparison of behavior frequencies among categories is justified.

Interactions With Other Birds

Although direct interactions with other bird species at migration stopovers were infrequent, all observers recorded occasional interspecific aggression. At roost sites the cranes occasionally chased mallards (*Anas platyrhynchos*), snow geese (*Chen caerulescens*), or other waterfowl species by running at them with wings raised. Juvenile R-Y frequently performed such behavior (Stehn 1984). Usually waterfowl were tolerated at close range, although the cranes occasionally chased other species such as gulls (*Larus* spp.), black-billed magpies (*Pica pica*), and sandhill cranes (*Grus canadensis*). Ground crews did not observe other species chasing whooping cranes. In one unusual case, a great blue heron (*Ardea herodias*) foraged with a family group of whooping cranes in several fallow or stubble fields and then roosted within 10 m of the cranes for one night (Smith 1983). There was little evidence that whooping cranes sought out the company of sandhill cranes, although both species sometimes foraged or migrated in close association.

The maximum number of cranes observed together on the migration route was seven (during much of the 1984 spring migration of family 19/83). Birds that associated with family groups were periodically chased during close approach. Smith (1983) reported that the largest parent of family 10/82 (probably the male) would chase the largest of three other cranes that associated with them in Saskatchewan while the smaller parent would chase the smallest of the three. Although chases sometimes occurred

Table 6. *Average number of hours of diurnal feeding, flying, and resting per day for migrating, radio-marked whooping cranes,[a] spring and fall, 1982–84.*

Analysis category	Number of days with data[b]	$\bar{X}$ Hours/day (±SD)			
		Fly	Feed	Rest	Feed and rest[c]
Fall 1982					
Family 10/82	17	3.9±3.8	4.6±2.9	3.8±1.2	1.7±2.7
Family 6/82[d]	8	5.5±3.9	3.5±2.1	3.8±1.3	1.2±2.3
Family 1/82[e]	6	0.0	6.4±1.6	7.3±1.9	0.0
Subadult 7/81	6	0.8±1.9	5.8±1.5	5.6±1.8	0.0
Canada only (families combined)	23	1.3±2.4	6.1±1.7	5.1±2.1	0.7±1.7
United States only (families combined)	14	6.3±3.7	2.8±2.2	3.4±1.5	1.6±2.8
Entire route (families combined)	37	3.2±3.8	4.9±2.5	4.5±2.0	1.1±2.2
Spring 1983 and 1984					
Family 10/82	2	7.3±2.1	3.9±0.5	1.3±1.7	0.0
Family 19/83	3	5.4±2.2	3.3±1.4	1.8±1.5	2.1±2.8
Subadults 10/82, 2/82	13	1.7±3.3	3.3±2.4	6.2±3.4	2.1±2.9
Entire route (families combined)	18	2.9±3.7	3.4±2.1	5.0±3.5	1.8±2.7

[a] Based on timelines developed from field journals.
[b] Days for which no more than 2 daylight hours were unaccounted.
[c] Represents resting wetlands where occasional feeding took place.
[d] Tracked primarily in the United States.
[e] Tracked only in Saskatchewan.

Table 7. *Allocation of time among categories of behavior by migrating radio-marked whooping cranes, 1982–84.*

Analysis category	Number of hours	Percent of time										
		No data	Forage	Agonistic	Stand	Alert	Walk	Fly	Dance	Preen	Rest	Other
Fall												
Parents	229.0	6.0	38.2	0.2	9.9	21.9	10.7	3.0	0.3	9.3	0.4	0.1
Subadults	117.4	4.8	41.9	0.1	14.7	12.6	11.9	2.0	0.2	10.0	1.7	0.0
Juveniles	127.4	6.6	51.9	0.0	10.8	8.1	10.0	2.8	0.1	8.8	0.7	0.1
Spring												
Parents	163.9	10.3	43.9	0.0	13.6	4.6	11.3	1.2	0.3	11.6	2.8	0.4
Subadults	175.8	10.6	29.6	0.1	16.0	7.0	11.9	1.5	0.7	14.5	7.6	0.5
Juveniles	89.2	11.0	49.2	0.1	11.3	2.1	8.6	1.3	0.1	8.4	3.3	4.6
Total	902.6											
Averages		8.2	41.1	0.1	12.7	10.6	10.9	2.1	0.3	10.7	2.8	0.7

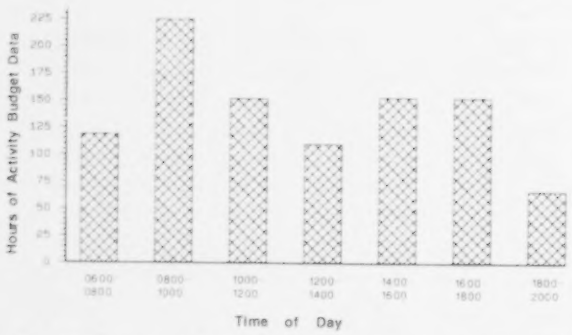

Fig. 10. Frequency distribution of the number of bird-hours of time-activity budget data taken for whooping cranes during the radio-tracking project, summarized for 2-h blocks, 0600–2000 h. Data are pooled for all age classes and seasons.

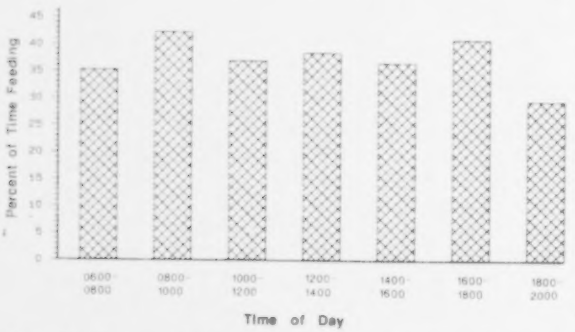

Fig. 11. Frequency distribution of percent of time whooping cranes were feeding, based on time-activity budget data (Fig. 10) and summarized for 2-h blocks, 0600–2000 h. Data are pooled for all age classes and seasons.

at distances up to 20 m, at other times birds foraged together without aggression.

In one anomalous situation, after the larger parent of family 1/82 sustained an injury from a possible golden eagle (*Aquila chrysaetos*) attack, this family and two other whooping cranes remained at the roost site for 2 days instead of flying to a nearby wheat field where they had foraged previously. Apparently, the behavior of not only family members but also the other two birds was influenced by that of the injured bird. Later, disturbance by hunters resulted in the parents becoming separated from the chick and the other cranes. Until the tracking effort shifted to another family 2 days later, the chick associated only with its "foster parents." On arrival at ANWR, field crews could not determine if the two adults associating with the chick were its true or foster parents.

Development of Independence in Juveniles

The radio-tracking of two family groups in spring 1983 (juveniles W-R and G-W/R) and one family group in spring 1984 (juvenile R-Y) revealed information on timing of parent–offspring breakup and development of independence in juveniles (Stehn 1983, 1984). During migration, field crews noticed an increase in the frequency of parental aggression toward their young in the families of W-R (15 incidents) and R-Y (13 incidents).

Types of aggression ranged from "aggressive walking" to jumping and kicking at the juvenile and, more frequently, pecking. Most aggression occurred during feeding, but the male parent of W-R followed a bout of dancing behavior with four threats directed toward W-R. Twelve of the 15 incidents in the W-R family were observed during a 3-day period in Saskatchewan. Overall,

in the W-R family, the female parent was the aggressor eight times and the male seven. Aggressive acts were typically brief and the birds immediately resumed normal, nonagonistic interactions as a family group. During all spring migrations, field crews recorded only two instances of parental feeding of the juvenile: W-R's parents fed it on 13 and 20 April 1983.

Other evidence of weakening of the parent–offspring bond was more subtle and difficult to quantify. Stehn (1983) noted a decrease over time in the synchronization of the behavior of parents and juvenile in the W-R family. This was particularly evident after W-R sustained a foot injury on 23 April. In another family, juvenile R-Y increased its foraging distance from its parents up to 50 m by 22 April after the family arrived in Saskatchewan.

Some data were obtained on the breakup of three families, involving juveniles R-Y, W-R, and G-W/R. The breakup of the R-Y family occurred on 26 April, following initiation of a migration flight from Spruce Lake, Saskatchewan. When the air crew located R-Y, it was flying alone in an erratic path that ended 3 h later, 40 km southeast from the point of origin. The next day, R-Y made several shorter flights, stopping once at Spruce Lake, before continuing to the Glaslyn area. It remained there alone until 9–11 May and disappeared until biologists located it at WBNP on 18 May. R-Y apparently had no further association with its parents after 26 April. The breakup of the W-R family occurred sometime between 1 May, when the family departed Meadow Lake, Saskatchewan, and 9 May, when the parents were found alone on their nesting territory. Biologists located W-R 17 km south of its natal territory on 28 May. Juvenile G-W/R accompanied its parents throughout the entire migration in spring 1983. Air crews followed this family to WBNP, where they arrived on 22 April, landing in an area traditionally used by nonbreeders about 17 km from the natal territory. On 23 April all three birds were in the natal territory, G-W/R standing about 20 m from its parents. Because further observations were not possible, the time when this family broke up was unknown. On 3 May, G-W/R appeared at the site where the family had originally landed on 22 April.

Response to Human Influences

Wariness in the presence of human activity, roads, and habitations varied considerably as a function of familiarity with a site (Stehn 1983), frequency of disturbance and, probably, individual variation in tolerance (Smith 1983). Generally it was not possible to evaluate tolerance quantitatively, except to determine the distances between feeding or roosting sites and the nearest road or habitation. Summaries from the appendix (Table A1) yield a mean distance from roost sites to the nearest road of 0.5 km (minimum = 50 m, $N = 33$) and a distance to the nearest habitation of 1.3 km (minimum = 150 m, $N = 20$). For feeding sites (Table 2A) mean distance to the nearest road was 0.4 km (minimum = adjacent, $N = 51$), and the nearest farmhouse was 1.8 km (minimum = 100 m, $N = 34$).

More direct evidence of wariness is revealed by anecdotal accounts of flushing due to human disturbance. This response varied greatly among individuals and families. For example, most birds tolerated moving vehicles at distances of 100 m or less, but family 6/82 flushed when vehicles approached at 200–400 m. Flushing distances tended to be greater when vehicles came to a stop or discharged occupants; however, family 10/82 tolerated ground crew members at 40 m during field foraging. Ward (1984) commented that whooping cranes increased their distance when human activity was high but often approached human activity closely when visually screened by vegetation or topography. The cranes usually ignored fixed-wing aircraft but reacted with alarm (one observation) to a helicopter.

Biologists have recently recognized the threat of power lines to flying cranes (Whooping Crane Recovery Team 1986; Faanes 1987), and that whooping cranes may be particularly vulnerable (Brown et al. 1987). This danger exists throughout the migration corridor. Two of the first three radio-marked chicks died as a consequence of collisions with power lines. Early in its first migration, chick R/W-G apparently struck a power line near Glaslyn, Saskatchewan, on 11 October 1981 (Vandel 1981). The power line was a single strand, 30 m high, and stretched between poles 100 m apart. The bird was treated by a veterinarian but died 1 week later. Chick W-R, after completing its first two migrations, was found dead under telephone lines near Waco, Texas, on 16 October 1982. Ground crews did not directly observe either incident, nor did they report any near-collisions. Stehn (1984) reported that only three of the roost sites used by family 19/83 in spring 1984 were close to power lines. However, three ground crew members commented independently on the potential vulnerability of the cranes to collisions when flying through fog, when flushed by human disturbance near power lines, or when landing after dark. Family 6/82 continued migrating long after sunset on 1 November 1982, and landed in a small wetland near Eureka, Kansas, bordered by power lines (J. Goldsberry, personal communication). Ground crews also recorded two other instances of nocturnal migration.

The potential threat from hunters was prevalent through much of each fall migration; however, ground crews did not observe hunters firing at whooping cranes. Family 1/82 flushed five times when surprised at close range by waterfowl hunters, but no shots were fired. Many hunters indicated an awareness or appreciation of whooping cranes when questioned by members of the ground crews (Smith 1983).

Discussion

Opportunistic information collected before this study was sufficient to delineate the approximate geographic limits of the migration corridor (Allen 1952; Johnson and Temple 1980), to determine the timing of peak migrations at various latitudes (Allen 1952; Johnson and Temple 1980), and to develop a preliminary profile of habitat types used for feeding and roosting (Johnson and Temple 1980). All of this information is potentially biased by varying detection probabilities in different portions of the migration corridor. Much of the habitat data gathered (Johnson and Temple 1980) has been based on post hoc visitations to sites known to have been used sometime in the past. Habitat or water conditions may have changed between time of use and time of data collection. The present study overcame these biases by documenting complete sequences of migratory movements and habitat use by radio-tagged, color-marked birds. By monitoring birds daily, it was possible to collect data in a systematic fashion, much of it suitable for quantitative analysis.

Habitat Use

During migration, whooping cranes used a broad range of natural and man-modified wetlands (primarily palustrine) and croplands within the prairie system of the central United States and southern Canada. The only apparent requirement of all birds at stopovers is some type of wetland. Wetland use does not appear to be affected by substrate texture or turbidity. For feeding, the species has clearly learned to exploit cultivated grains, such as barley and wheat, which are widely available throughout most of the migration corridor. A similar transition from natural to man-produced food resources has been made successfully by sandhill cranes (Guthery 1976; Hoffman 1976; Lewis 1979; Melvin 1982; Krapu et al. 1984). Although data were not collected on the proportion of the diet attributable to grain crops, the observed high use of grain fields suggests that, contrary to the speculation of Allen (1952), whooping cranes are primarily granivorous during migration.

Lacking quantitative data on habitat availability, it could not be determined whether habitats used were preferred habitats—cranes may have used certain habitats simply because preferred habitats were no longer available. Nonetheless, within the habitat use spectrum, cranes in this study showed certain patterns of habitat selection, subject to the cautions that (1) univariate analysis does not reveal the correlation structure of the variables treated here, and (2) the data are not derived from a random sample of individuals but rather from repeated observations of a small number of individuals. Cranes used temporary wetlands more frequently in spring; however, this may simply have been a consequence of the wetter conditions that are more prevalent in spring. A subtle difference in habitat use by family groups and nonfamilies emerged: family groups appeared to choose more heavily vegetated wetlands for roosting than birds without young. Also, 67% of family feeding sites were wetlands, compared with only 30% for nonfamilies. Several interpretations of these data are possible. Vegetated wetlands may provide better cover for young birds, reducing detectability by predators. The high incidence of foraging in wetlands probably reflects, in part, use of roosting wetlands for feeding. Juvenile birds may require longer feeding bouts than adults, due to growth requirements and lower foraging efficiency. Furthermore, the more vegetated wetlands used by families may yield higher densities of protein-rich invertebrates and small vertebrates important to fall juveniles that are not fully grown. As most of the data came from fall observations, it was not possible to compare statistically the use of vegetated wetlands by family groups between spring and fall.

Proximity of feeding and roosting sites seems to be important; 56% of all paired feeding-roosting sites were <1 km apart. Often the cranes walked from a roosting wetland to a nearby field to feed. The impressions of the ground crew biologists, supplemented by the examination of topographic maps, indicate that such situations are readily available throughout much of the migration corridor. Availability of large wetlands did not seem to be critical for cranes observed in this study, as 41% of the wetlands used for roosting were smaller than 0.5 ha. Fifteen percent were smaller than 0.1 ha. The birds did occasionally use large wetlands, such as many of the large lakes in southern Saskatchewan and impoundments at Quivira NWR and Cheyenne Bottoms, Kansas. The overall infrequent use of large wetlands may simply reflect their scarcity in many areas.

Behavior and Time Allocation

Although general patterns emerged from construction of timelines based on field notes, variability in sequence and duration of bouts of feeding, resting, and flying seemed to be the rule (Table 6; Fig. 9). Cranes deserted

roost ponds shortly before or after sunrise and often did not return until sunset. Feeding, the dominant diurnal activity of all cranes, averaged 1–5 h per day in up to six bouts, interrupted by periods of resting. The timelines suggest a higher frequency of feeding in fall, possibly related to the prolonged "staging" period in Saskatchewan. There, because birds usually remained at one site for 2 or 3 weeks, flying time contributed little to daily activity.

The time-activity budget data, which best define how cranes allocated time among activities, lend weak support to the concept of higher feeding rates in fall (3.8% more total feeding time in fall for all categories of birds). These data also show an inconsistency among bird categories: parent birds fed less frequently in fall than in spring; subadults fed more frequently in fall. Increased feeding by parents in spring may be related to the more rapid migration of breeding pairs. When spring and fall values were combined, the parent-to-subadult ratio for foraging time (1.17:1) was almost identical to the parent-to-subadult ratio in wintering sandhill cranes in western Texas (Tacha 1987).

Similarly, averages of fall and spring data yielded a juvenile-to-parent ratio of 1.25:1 for foraging time, identical to winter values for sandhill cranes in western Texas (Tacha 1987). A decrease in that ratio between fall and spring resulted from changes in the frequency of feeding by parents rather than juveniles. At all times juveniles fed more often than adults. Young birds are probably inefficient foragers and may still be growing in the early stages of their first migration—both factors result in more time allocated to foraging. Parental vigilance in fall presumably enables young to devote more time to foraging without substantially increasing the risk of predation. Continuation of the high juvenile foraging rate into spring suggests that birds may require more than one migration to achieve peak foraging efficiency.

Dancing behavior during migration probably serves primarily as a mechanism of pair formation, as it was found to be least frequent in juveniles and most frequent in spring subadults. This is consistent with G. Archibald's (cited in Johnsgard 1983) observation that dancing is most frequent in 2- to 3-year-old unpaired cranes. Tacha (1988) also reported a higher rate of dancing in subadult sandhill cranes; however, dancing can occur almost anytime and be performed by any bird (Blankinship 1976; Johnsgard 1983). Its function in any particular context must be evaluated cautiously.

A decline in the incidence of alert behavior occurred in all categories of birds between fall and spring. This may have been in part an artifact of the subset of individuals radio-tracked—spring birds in this study usually had more experience with migration than fall birds. The level of wariness exhibited by any bird is likely to decrease as a function of habituation to surroundings or degree of experience. Within the family group, a decrease in alert behavior by parents may be indicative of a weakening family bond. A weakening of the bond is also suggested by an increase in parent–offspring conflict and wandering tendency of juveniles as spring migration progresses. Based on three family groups observed in this study, the family may break up during migration or after arriving at WBNP. Stehn (1984) suggested that the timing of breakup may be related to the sex of the juvenile. Higher levels of aggression in juvenile males may tend to promote an earlier dissolution of the family than might occur with juvenile females. However, the sexes of juveniles observed in this study were not known. An accurate method for sexing crane chicks would be helpful in determining whether a sex bias exists in the timing of family breakup.

Vulnerability and Mortality

The primary threat to migrating whooping cranes observed in this study was collision with power lines. Power line collisions caused the death of one juvenile and one subadult. Although this can be extrapolated to a power line kill rate of one death per 10.2 crane-years (based on the radio-marked sample of nine fledged birds as of February 1987), it represents one-third of the deaths of radio-marked birds in this study. Power line collisions have been implicated in at least 13 whooping crane deaths nationwide, including the experimental Grays Lake population (Fjetland 1987). The hazard remains a significant factor affecting long-term recovery of the whooping crane.

Although hunters flushed cranes on several occasions in the radio-tracking study, field crews did not detect gunfire in the vicinity of the birds. The closest encounter was with a hunter who had placed decoys near roosting birds before dawn and was undetected by the birds until daylight. This illustrates the potential hazard from hunters and the need for continuing hunter education within the migration route of whooping cranes. Fortunately most hunters interviewed were aware of—and sympathetic to—the whooping crane and its status. Except for one recent case near ANWR (January 1989; J. Lewis, personal communication), there is no record of a hunter killing a whooping crane since 1967–68 (Whooping Crane Recovery Team 1986), despite widespread potential exposure to hunting pressure (Konrad 1987; Thompson and George 1987).

The risk of predation to postfledging whooping cranes is probably minimal. Golden eagles are potentially the

most significant predators. Windingstad et al. (1981) reported an observation of this species attacking a juvenile whooping crane in flight, resulting in the crane's death. In the present study, field crews believed that an injured male parent (family 1/82) had been wounded by a golden eagle observed in the vicinity. After the apparent predation attempt, the injured bird exhibited alarm behavior in response to flying golden eagles, but not to bald eagles (*Haliaeetus leucocephalus*; Smith 1983). This incident may have led to the dissociation of the juvenile from its parents. At least one radio-marked juvenile at ANWR was believed to have been killed by an avian predator, perhaps a great horned owl (*Bubo virginianus*; T. Stehn, personal communication).

Of the 12 deaths of radio-marked birds in this study, 6 happened at WBNP before fledging. Most of these six are attributed to wolf (*Canis lupus*) predation. They occurred in 1982 and 1983, 2 drought years when wolves had ready access to many crane breeding territories, and predation was high on both radio-marked chicks and chicks that were only color-banded (E. Kuyt, personal communication). Of the nine radio-marked chicks that fledged, one died from a power line collision during its first migration, a second died after a similar collision during its second fall migration, and four died or disappeared on the wintering grounds at ANWR. Of the last four chicks, two died during their first winter, one during its second winter, and the fourth during its third winter (T. Stehn and E. Kuyt, personal communication). Suspected causes of two of the winter deaths were predation and avian tuberculosis. The annual mortality of the nine fledged radio-marked birds was 14.5%, weighted by the number in each cohort and the age of each cohort in February 1987.

Biologists have often expressed concern about the possible injurious effects of radio-packages or the handling of birds during radio application. Kuyt and Goossen (1987) compared survival of radio-marked birds with color-banded birds from the 1982 cohort and determined that the radio-marked sample suffered significantly higher mortality by the end of 1983. By using data from the entire study, I compared survival of radio-marked birds with an estimate of annual survival in the entire population based on data from the ANWR wintering flock (Whooping Crane Recovery Team 1986). The data used were records of numbers of birds arriving and departing ANWR, 1977–86. These records included birds of all age classes and yielded an annual, postfledging mortality estimate of 6.1%. Because these records did not take into account juveniles that died before reaching ANWR, I deleted the one such case from the radio-tracking study and redetermined the annual mortality of postfledging radio-marked birds to be 13.9% instead of 14.5%.

The annual mortality estimate derived from less accurate 1938–85 ANWR figures is 8.6%. Therefore, it is likely that the true long-term mortality rate of birds that reached ANWR at least once is between 6.1% and 8.6%, 5.3–7.8% less than the estimate from the radio-marked bird study. This difference, however, does not suggest a higher loss of radio-marked birds. First, the estimates of mortality for the small sample of only eight radio-marked birds would change substantially with the chance death or survival of only one bird. Second, the estimate for radio-marked birds is based on young age classes, the oldest surviving bird being only 5.5 years old. Higher mortality is normally expected in younger birds. For example, ANWR's 1938–85 records show that mortality of juvenile birds during their first winter was 3 times greater than that of the wintering flock as a whole (Whooping Crane Recovery Team 1986). Survivorship models developed by Binkley and Miller (1980) for whooping cranes likewise show a high first-year mortality followed by a sharp drop in subsequent years. Of the deaths of all fledged, radio-marked birds in the present study, three occurred in the first year of life, two in the second year, and one in the third year. There have been no deaths since November 1984. If the three surviving radio-marked birds (ages 3.5, 4.5, and 5.5 years in February 1987) live to be 10 years old, the annual mortality estimate from radio-marked birds would drop to 6.6%. Hence, the evidence that radio-marking affects the survival of postfledging whooping cranes is marginal.

Distribution, Tradition, and Management

Complete stopover information between ANWR and central Saskatchewan was obtained for four crane groups in fall and three in spring. The distribution of stopovers in the United States was skewed toward Kansas and Nebraska in spring and Oklahoma and Texas in fall. The distribution of crane use-days was similar. All States from Texas to North Dakota received at least some use by radio-tracked birds in both seasons. Family 7/81 stopped once in northeastern Montana in fall 1981. Inclusion of Saskatchewan in State and provincial distribution summaries resulted in a distribution of crane use-days highly skewed toward Saskatchewan in both seasons and a distribution of stopovers similarly skewed for fall migration only. The United States received proportionately more use in spring than in fall.

Previous concepts of whooping crane distribution in migration have been based on compilations of incidental

Table 8. *Geographic distribution of incidental sightings of migrating whooping cranes in the United States[a] compared with that of crane group-use-days from the present study.[b]*

	Incidental sightings				Dedicated sightings (group-use-days)	
	1975–82[c]		1950–79[d]		1981–84[e]	
Area	*N*	(%)	*N*	(%)	*N*	(%)
Texas	4	2.4	2	0.7	19	19.2
Oklahoma	17	10.6	24	8.8	11	11.1
Kansas	30	18.6	60	22.1	25	25.3
Nebraska	29	18.0	39	14.4	27	27.3
South Dakota	14	8.7	33	12.1	7	7.1
North Dakota	63	39.2	92	33.8	8	8.1
Montana	4	2.5	22	8.1	2	2.1

[a] Johnson and Temple 1980; D. K. Arhart, memorandum to Director, U.S. Fish Wildl. Serv., 11 June 1982, in files at Patuxent Wildlife Research Center, Laurel, Md. 20708.
[b] Group-use-day is defined as one group of cranes using one site for 1 day. Data presented from this study include only complete radio-trackings for four fall and three spring groups.
[c] D. K. Arhart, memorandum to Director, U.S. Fish Wildl. Serv., 11 June 1982, in files at Patuxent Wildlife Research Center, Laurel, Md. 20708.
[d] Johnson and Temple 1980.
[e] Present study.

sightings (Johnson and Temple 1980). The distribution of incidental sightings is biased by distribution of observers, thereby favoring urban centers or popular wildlife observation areas such as National Wildlife Refuges; however, there should be no bias in the distribution of stopovers of radio-marked birds except that resulting from small sample size. Comparison of radio-tracking results with two independent data sets of incidentally sighted cranes (Johnson and Temple 1980; D. K. Arhart, memorandum to Director, U.S. Fish Wildl. Serv., 11 June 1982, in files at Patuxent Wildlife Research Center, Laurel, Md. 20708) illustrates the expected discrepancy (Table 8). Only United States data are shown because of the inconsistent availability of Saskatchewan records. Numbers of incidental sightings of cranes are compared with crane group-use-days from the present study, using the assumption that probability of incidental sightings is a function of length of stay at a stopover but not of the number of birds in a group (length of stay of incidentally sighted birds was not usually known). Although 30.3% of the crane group-use-days from the radio-tracking study were in Texas and Oklahoma and 8.1% in North Dakota, respective values from incidental sightings were 9.5% and 33.8% (Johnson and Temple 1980) and 13.0% and 39.2% (D. K. Arhart, memorandum to Director, U.S. Fish Wildl. Serv., 11 June 1982, in files at Patuxent Wildlife Research Center, Laurel, Md. 20708). This suggests that migrating whooping cranes are underreported from Texas and Oklahoma and overreported from North Dakota. As there is no obvious correlation with human population density, the reasons for the reporting pattern are unclear. Nonetheless, it is likely that the distribution resulting from radio-tracking is a more accurate representation of the "true" distribution of cranes.

Johnson and Temple (1980) concluded that there are no critical, traditional wetlands used by migrating whooping cranes. The results of the present study lead to the same conclusion, as individuals did not use the same stopovers in different migrations, and groups migrating independently rarely shared stopovers used by other groups. There is evidence from incidental sightings over the years (Allen 1952; Johnson and Temple 1980; D. K. Arhart, memorandum to Director, U.S. Fish Wildl. Serv., 11 June 1982, in files at Patuxent Wildlife Research Center, Laurel, Md. 20708; Didiuk 1986) that certain large wetlands are used by whooping cranes (not necessarily the same individuals) on a fairly regular, but not annual, basis. Examples of such wetlands are Salt Plains NWR, Oklahoma; Cheyenne Bottoms, Kansas; Platte River, Nebraska; Byers Lake, Texas; and Last Mountain Lake, Saskatchewan. However, repeated use of such wetlands can be expected in any species that traverses a narrow migration corridor. This is particularly true where wetlands are infrequently encountered, such as the south-

ern Great Plains. The evidence from this study supports the notion that repeated use of sites is primarily a random phenomenon.

Despite a lack of dependence on specific wetlands, migrating whooping cranes traditionally spend at least 2–3 weeks in fall in the Saskatchewan agricultural district before continuing rapidly to Texas (Kuyt 1987; present study). The core area in Saskatchewan encompasses at least 85,000 km^2 (Didiuk 1986; B. Johns, personal communication), and therefore does not meet the criterion of geographic discreteness implicit in the definitions of staging areas or traditional stopovers used for sandhill cranes (Melvin and Temple 1981; Krapu 1987). However, the region probably serves the same function as for sandhill cranes (Tacha et al. 1985): providing the abundant food resources necessary for rapid lipid deposition. The cropland region of Saskatchewan is the first food-rich zone to be encountered south of the breeding grounds, where late summer drought typically limits foraging opportunities. In exceptionally wet years, the whooping cranes sometimes remain at WBNP later than normal and spend correspondingly less time in the Saskatchewan grain fields (E. Kuyt, personal communication). Use of Saskatchewan in spring is more abbreviated, yet is long enough (Table 2) to suggest it also may be a period of lipid buildup, anticipatory to arrival at the breeding grounds. If so, it would be the only location along the migration route remotely comparable to the spring staging phenomenon of sandhill cranes in Nebraska (Krapu 1987; Tacha et al. 1987).

Given an opportunistic pattern of wetland use and the absence of clearly defined, traditional staging areas, how does one develop an effective management strategy for migrating whooping cranes? Clearly, even though there are no recent records of hunter kills, hunter education and enlightened management of hunting seasons within the migration corridor (Thompson and George 1987) need to be continually stressed. Research on factors responsible for collisions with power lines and development of creative modifications of power lines to minimize strike potential also need increased emphasis. Habitat management, on the other hand, presents a more difficult problem. As whooping cranes require wetlands at all stopovers, any steps taken to ensure wetland availability throughout the corridor would be helpful. Private farm and ranch owners could be encouraged through the Food Security Act of 1985 (Farm Bill) to maintain their wetlands as whooping crane stopover habitat, especially those that meet the criteria identified as usable by whooping cranes. In some situations, unsuitable wetlands might be rendered usable by removal of emergent vegetation stands. Other legislated incentives would be needed in Canada to encourage landowners in the staging region to protect wetlands.

State and Federal programs dedicated to impoundment management for whooping cranes would be an essential supplement to any voluntary programs under the Farm Bill. Although whooping cranes do not require large wetlands, such wetlands would be more easily detected by migrating cranes. Despite a low probability of regular use by whooping cranes, proper management of these impoundments would also serve to benefit other wetland species, particularly waterfowl and shorebirds. Many such impoundments already exist, although some are perpetually threatened by water diversion for agriculture. An expanded system throughout the migration corridor—focused in the intensively used areas of Saskatchewan and the most arid portions of the Great Plains—would serve as insurance against both severe drought and excessive drainage of natural wetlands.

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Appendix. Locations and characteristics of sites used by radio-marked whooping cranes.

Table A1. *Locations and characteristics of overnight roosting wetlands used by radio-tracked whooping cranes (*Grus americana*).*

Year; color band combination[a]	Roost number	Location	Ownership	Dates of use	Wetland area (ha)	Wetland classification[b]	Dominant vegetation	Distance to road/farm
Fall 1981								
R/W-G	1	11 km N Glaslyn, Sask.	Public	27 Sept.–9 Oct.	>250	Palustrine, perm. flooded	*Typha* sp.	500 m/1 km
	2	11 km N Glaslyn, Sask.	Private	27 Sept.–11 Oct.	0.5	Palustrine	*Myriophyllum* sp.	250 m/500 m
W-R/W	3	5 km E, 3 km S Reward, Sask.	Private	10, 11 Oct.	2	Palustrine	*Typha* sp.	100 m/3 km
	4	6 km NW Luseland, Sask.	Private	11–20 Oct.	1	Palustrine	*Beckmannia* sp.	1 km/1 km
	5	6 km NW Luseland, Sask.	Private	11–20 Oct.	0.5	Palustrine, temp. flooded	Barley	600 m/1 km
	6	5 km SE Neville, Sask.	Private	10, 21 Oct.	8	Lacustrine	*Carex* sp.	2 km/3 km
	7	S Plentywood, Mont., on the Poplar River	Private	21, 22 Oct.	40–50 m wide	Riverine	NR[c]	NR/3.2 km
	8	11 km S Merritt Reservoir, Neb.	Private	22, 23 Oct.	6	Palustrine	*Scirpus* sp.	100 m/1 km
	9	3 km NW Oconto, Neb.	Private	23, 24 Oct.	0.25	Palustrine, artificially flooded impoundment	*Sagittaria* sp.	NR
	10	15 km SW Rush Center, Kans.	Private	24, 25 Oct.	NR	Palustrine, artificially flooded impoundment	NR	NR
	11	5.5 km SW Waynoka, Okla.	Private	25, 26 Oct.	40–50 m wide	Riverine	NR	500 m to railroad
	12	24 km SE Lawton, Okla.	Private	26, 27 Oct.	0.5	Palustrine	*Cyperus* sp.	50 m/500 m
	13	8 km W Byers, Tex.	Private	27 Oct.–1 Nov.	2	Palustrine	*Xanthium* sp.	300 m/200 m
	14	8 km NW Byers, Tex.	Private	27 Oct.–1 Nov.	80–100 m wide	Riverine, perm. flooded	*Larix* sp.	300 m/1 km
	15	8 km SE Rosebud, Tex.	Private	1, 2 Nov.	0.25	Palustrine, artificially flooded impoundment	*Sagittaria* sp.	600 m/200 m

Table A1. *Continued.*

Year; color band combination[a]	Roost number	Location	Ownership	Dates of use	Wetland area (ha)	Wetland classification[b]	Dominant vegetation	Distance to road/farm
	16	3 km NW Tivoli, Tex.	Private	2, 3 Nov.	20	Palustrine, temp. flooded	Coastal bermuda grass	200 m/ 400 m
Fall 1982								
W-R/W	17	10 km W, 9 km S Watrous, Sask., west bank of lake	Private	18 Sept.–5 Oct.	NR	Lacustrine, saline alkali flats	*Salicornia* sp.	NR
	18	0.8 km NW site 17	Private	6, 7 Oct.	NR	Lacustrine, saline alkali flats	*Salicornia* sp.	NR
	19	0.4 km E site 17	Private	8–10 Oct.	NR	Lacustrine, saline alkali flats	*Salicornia* sp.	NR
W-R	20	5 km N Fairholme, Sask.	Private	11, 12 Oct.	>1,500	Lacustrine	*Eleocharis* sp.	NR
	21	8 km N Fairholme, Sask.	Public	13 Oct.	>1,500	Lacustrine	*Eleocharis* sp.	NR
	22	177 km S, 37 km W Watrous, Sask.	Private	14 Oct.	NR	Palustrine, season flooded	Algae	NR
	23	6.4 km SW Rabbit Lake, Sask.	Private	15 Oct.	NR	Palustrine, semi-perm. flooded	*Carex* sp.	NR
	24	11.6 km N, 1.9 km W St. Walburg, Sask.	Private	16 Oct.	NR	NR	NR	NR
	25	29 km N, 3.2 km W Lashburn, Sask.	Private	17 Oct.	NR	NR	NR	NR
	26	17.7 km NW S. Battleford, Sask.	Private	18–26 Oct.	NR	Palustrine, semi-perm. flooded	*Typha* sp.	NR
	27	N Gibson Creek, approx. 10 km NW Radville, Sask.	NR	27 Oct.	NR	NR	NR	NR
	28	1.9 km NE Golden Valley, N. Dak.	Private	28 Oct.	NR	Palustrine	NR	NR
	29	NR (S. Dak.)	Private	29 Oct.	NR	NR	NR	NR
	30	1.2 km NW junction hwys. 253 and 47 between Eureka and Bowdle, S. Dak.	Private	30 Oct.	2	Palustrine, marsh	*Sagittaria* sp.	NR

Table A1. *Continued.*

Year; color band combination[a]	Roost number	Location	Ownership	Dates of use	Wetland area (ha)	Wetland classification[b]	Dominant vegetation	Distance to road/farm
	31	7.2 km NW Haven, S. Dak.	Public	31 Oct.	60	Palustrine	*Scirpus* sp.	NR
	32	approx. 24 km SE Ainsworth, Neb.	NR	1 Nov.	NR	NR	NR	NR
	33	W Albert, Okla. in Swan Lake community	Public	2 Nov.	"Large reservoir"	Lacustrine	*Scirpus* sp.	NR
	34	approx. 8 km NW Vidaurri, Tex.	Private	3 Nov.	NR	NR	NR	NR
W/R-G	35	SW tip Indi Lake, 7 km NW Hanley, Sask.	Public—leased by Ducks Unlimited	15, 18–24 Oct.	300	Palustrine, intermit. exposed	*Scirpus americanus*	800 m/ 600 m
	36	7 km NW Hanley, Sask.	Private(?)	16, 17 Oct.	1.5	Palustrine, intermit. exposed	NR	900 m/ 3 km
	37	8 km NW Hanley, Sask.	Private(?)	23 Oct.	NR	Open ditch bank	NR	800 m/ 5 km
B/W-R	38	28 km ENE Lumsden, Sask.	Private	24, 25 Oct.	0.6	Palustrine, semi-perm. flooded	*Carex* sp.	NR
	39	7 km E Rt. 6 bridge over Quapelle River, Sask.	Private	26 Oct.	160	Lacustrine, artificially flooded	Submerged forb	NR
	40	7 km NW Colgate, Sask.	Private(?)	27 Oct.	1	Palustrine, intermit. exposed	NR	NR
	41	19 km SSW Pierre, S. Dak.	Private	28 Oct.	0.5	Palustrine, temp. flooded	*Agropyron smithii*	NR
	42	15 km SSE Colome, S. Dak.	Private	29 Oct.	0.03	Palustrine, intermit. exposed	*Spartina pectinata*	NR
	43	25 km SW Atkinson, Neb.	Private	30, 31 Oct.	2	Palustrine, intermit. exposed	*Spartina pectinata*	NR
	44	3 km NW Eureka, Kans.	Private	1 Nov.	0.2	Palustrine, artificially flooded	NR	NR
	45	15 km NNW Gainesville, Tex.	NR	2 Nov.	80–100 m wide	Riverine	NR	NR
Fall 1983								
G-W/R and W-R	46	Richardson Lake, Alta.	NR	24 Sept.	NR	Sand dune: 7.2 km long, 0.8–3.2 km wide; adjacent to muskeg	NR	NR

Table A1. *Continued.*

Year; color band combination[a]	Roost number	Location	Ownership	Dates of use	Wetland area (ha)	Wetland classification[b]	Dominant vegetation	Distance to road/farm
	47	St. Cyr Lake, Sask.	NR	25 Sept.	NR	Palustrine, semi-perm. flooded	NR	NR
	48	Witchekan Lake, Sask.	Indian reserv.	26 Sept.	NR	Palustrine, semi-perm. flooded	NR	NR
	49	Brownlee, Sask.	Provincial	27 Sept.–9 Oct.	NR	Palustrine, intermit. exposed	*Potamogeton* sp.	NR
	50	Brownlee, Sask.	Private	28 Sept.–8 Oct.	NR	Palustrine, intermit. exposed	*Eleocharis* sp.	NR
	51	Pelican Lake, Sask.	Private	10 Oct.	NR	Lacustrine, intermit. exposed	Algae	NR
	52	Isabel, S. Dak.	Private	11 Oct.	NR	Palustrine, perm. flooded	Algae	NR
	53	Wilson Lake, Kans.	Federal	12 Oct.	NR	Lacustrine, perm. flooded	NR	NR
	54	Salt Plains NWR, Okla.	Federal	13–16 Oct.	NR	Lacustrine, perm. flooded	*Scirpus* sp.	NR
	55	Salt Plains NWR, Okla.	Federal	17–19 Oct.	NR	Lacustrine, perm. flooded	*Scirpus* sp.	NR
	56	Jets, Okla.	Private	20 Oct.	NR	NR	NR	NR
	57	Salt Plains NWR, Okla.	Federal	21 Oct.	NR	Lacustrine, perm. flooded	NR	NR
	58	Lake Dallas, Tex. (in city of Dallas)	Private	22 Oct.	NR	Lacustrine, intermit. exposed	Buffalo burr	NR
	59	8 km W, 4.8 km S Sealy, Tex.	Private	23 Oct.	NR	Palustrine, intermit. exposed	NR	NR
	60	16 km NW Rockport, Tex.	NR	24 Oct.	NR	Estuarine, irregularly flooded	*Ephedra* sp.	NR
R-Y	61	Glaslyn, Sask.	Provincial	17 Oct.	NR	Lacustrine, intermit. exposed	Algal mat	NR
	62	Glaslyn, Sask.	Private	18–21 Oct., 23 Oct.–4 Nov.	NR	Lacustrine, intermit. exposed	*Myriophyllum* sp.	NR
	63	Last Mt. Lake, Sask.	Private	5, 6 Nov.	NR	Lacustrine, intermit. exposed	*Scripus* sp.	NR
	64	Long Lake NWR, N. Dak.	Federal	7 Nov.	NR	Lacustrine, artificially flooded	*Scirpus* sp.	NR
	65	Lake Oahe, S. Dak.	NR	8 Nov.	NR	Lacustrine	NR	NR

Table A1. *Continued.*

Year; color band combination[a]	Roost number	Location	Ownership	Dates of use	Wetland area (ha)	Wetland classification[b]	Dominant vegetation	Distance to road/farm
Spring 1983								
G-W/R	66	4 km SE Thrall, Tex.	Private	9, 10 Apr.	2	Palustrine, perm. flooded impoundment	*Eleocharis* sp.	Isolated
	67	7 km WNW Byers, Tex.	Private	10, 11 Apr.	0.5	Palustrine, season. flooded	*Eleocharis* sp.	NR
	68	22 km N Hoxie, Kans.	Private	11–14 Apr.	0.6	Palustrine, temp. flooded	*Eleocharis* sp.	300 m/NR
	69	3 km NE Hendley, Neb.	Private	14, 15 Apr.	0.2	Palustrine, intermit. exposed	NR	100 m/NR
	70	6 km N Callaway, Neb.	Private	15–17 Apr.	1	Palustrine, perm. flooded	*Polygonum* sp.	100 m
	71	9 km NNE Callaway, Neb.	Private	17, 18 Apr.	0.2	Palustrine, semi-perm. flooded	*Polygonum* sp.	200 m/NR
	72	7 km SSW Prairie City, S. Dak.	Private	18, 19 Apr.	80	Lacustrine, season. flooded	*Polygonum* sp.	NR
	73	35 km NW Williston, N. Dak.	Private	19, 20 Apr.	0.5	Palustrine, semi-perm. flooded	Dense aquatic plants	NR
	74	17 km SSW Biggar, Sask.	Private	20, 21 Apr.	1	Palustrine	*Glyceria* sp.	NR
	75	24 km N Fort McMurray, Alta.	NR	21, 22 Apr.	NR	Riverine, frozen	NR	NR
W-R	76	10 km SSE Electra, Tex.	Private	11, 12 Apr.	0.2	Palustrine, temp. flooded	Bunchgrass	350 m/NR
	77	3 km E Hazelton, Kans.	Private	12–16 Apr.	1.2	Palustrine, intermit. exposed	Winter wheat	180 m/NR
	78	Quivira NWR, Kans.	Federal	16, 17 Apr.	400	Palustrine, semi-perm. flooded impoundment	*Distichlis* sp.	185 m/NR (200 m to oil well)
	79	6 km WNW Glen Elder, Kans.	Private	17, 18 Apr.	0.1	Palustrine, perm. flooded impoundment	*Polygonum* sp.	NR/140 m
	80	27 km NE White River, S. Dak.	Private	18, 19 Apr.	0.5	Palustrine, perm. flooded impoundment	NR	3 km/NR
	81	13 km NW Williston, N. Dak.	Private	19, 20 Apr.	0.05	Palustrine, season. flooded	Submergents	180 m/ 230 m
	82	4 km NE Minton, Sask.	Private	20–30 Apr.	0.2	Palustrine, intermit. exposed	NR	800 m/ 800 m

Table A1. *Continued.*

Year; color band combination[a]	Roost number	Location	Ownership	Dates of use	Wetland area (ha)	Wetland classification[b]	Dominant vegetation	Distance to road/farm
	83	2 km N Rapid View, Sask.	Private	30 Apr.–1 May	0.5	Palustrine, intermit. exposed	Wheat stubble	800 m/800 m
Spring 1984 R-Y	84	8 km SW Apache, Okla.	Private	8, 9 Apr.	0.1	Palustrine, temp. flooded impoundment	NR	400 m/NR
	85	9.7 km E Dighton, Kans.	Private	9–13 Apr.	1.2	Palustrine, season. flooded	Winter wheat	400 m/NR
	86	12.9 km SE Hays, Kans.	Private	13, 14 Apr.	0.1	Palustrine, season. flooded impoundment	NR	100 m/NR
	87	17.7 km NNE Wakeeney, Kans.	NR	15, 16 Apr.	NR	NR	NR	NR
	88	4.8 km SW Alticane, Sask.	Private	18, 19 Apr.	0.04	Palustrine, season. flooded	Wheat stubble	400 m/NR
	89	6.4 km SW Spruce Lake, Sask.	Private	19–26 Apr.	0.05	Palustrine, season. flooded	Wheat stubble	250 m/NR
	90	Blaine Lake—4.8 km ESE Krydor, Sask.	Public	27–29 Apr.	1,200	Lacustrine, perm. flooded	NR	1 km/NR
G-W/R and W-R	91	7.2 km SW Lake Whitney Dam, Tex.	Private	9 Apr.	NR	Palustrine, intermit. exposed	NR	NR
	92	Okla., 14.5 km NE Ringgold, Tex.	Private	10 Apr.	NR	Riverine, perm. flooded	NR	NR
	93	5.2 km E Lake City, Kans.	Private	11, 12 Apr.	0.02	Palustrine, intermit. exposed impoundment	NR	300 m to power line
	94	Lake City, Kans.	Private	13–16 Apr.	NR	Palustrine, intermit. exposed	*Eleocharis* sp.	NR
	95	Cedar Bluff Reservoir, Kans.	Federal	17 Apr.	NR	Lacustrine, semi-perm. flooded	*Typha* sp.	NR
	96	17.7 km WNW North Platte, Neb. 0.8 km N of Platte River	Private	18(?)–19 Apr.	NR	Palustrine, intermit. exposed	Grass	NR
	97	Near site 96, Neb.	Private	20, 23 Apr.	0.07	Palustrine, intermit. exposed	Grass	NR

Table A1. *Continued.*

Year; color band combination[a]	Roost number	Location	Ownership	Dates of use	Wetland area (ha)	Wetland classification[b]	Dominant vegetation	Distance to road/farm
	98	Near site 96, Neb.	Private	21, 22 Apr.	"Small pond"	Palustrine, intermit. exposed	Grass	NR
	99	Near site 96, Neb.	Private	23, 27 Apr., 7 May	0.6	Palustrine, temp. flooded	Grass	NR
	100	Near site 96, Neb.	Private	24 Apr.	0.01	Palustrine, temp. flooded	Grass	NR
	101	Near site 96, Neb.	Private	25, 26 Apr.	8.8	Palustrine, temp. flooded	Grass	NR
	102	Near site 96, Neb.	Private	5 May	0.04	Palustrine, temp. flooded	Grass	NR
	103	NR (Neb.)	Private	6 May	5.3	Palustrine, temp. flooded	Grass	NR
	104	Near Dickinson, N. Dak.	Private	9, 10 May	NR	Palustrine, semi-perm. flooded	*Scirpus* sp.	0.8 km to power line
	105	Near Williston, N. Dak.	Federal	11 May	NR	Riverine, perm. flooded	*Typha* sp.	NR
	106	Dilke, Sask.	Private	13 May	NR	Lacustrine, perm. flooded	NR	NR

[a] Colors: white, red, green, blue, yellow. Combination order: Upper/lower left leg-upper/lower right leg.
[b] After Cowardin et al. 1979.
[c] NR = not recorded.

Table A2. *Locations and characteristics of feeding sites used by radio-tracked whooping cranes.*

Year; color band combination[a]	Site number	Location[b]	Ownership	Dates of use	Cover type	Size (ha)	Shape	Foods	Distance to road/farm
Fall 1981									
R/W-G	1	1 km from roost 1	Private	26 Sept.–11 Oct.	Chisel-plowed barley	32	Rectangular	Abundant waste grain	500 m/ 1 km
	2	1 km from roost 2	Private	26 Sept.–11 Oct.	Chisel-plowed barley	80	Rectangular	Abundant waste grain	250 m/ 500 m
W-R/W	3	1 km from roost 1	Private	8 Oct.	Barley stubble	80	Rectangular	Waste grain	250 m/ 1 km
	4	1 km from roost 1	Private	9 Oct.	Chisel-plowed barley	80	Rectangular	Waste grain	250 m/ 1 km
	5	1 km from roost 3	Private	10 Oct.	Wheat stubble	7,250	Rectangular	Abundant waste grain	100 m/ 3 km
	6	1 km E roost 3	Private	10 Oct.	Dry wetland	2	Round	NR[c]	500 m/ 3 km
	7	1 km E, 0.5 km S roost 3	Private	11 Oct.	Dry wetland	4	Oval, irregular	NR	Adjacent/ 3 km
	8	1 km N roost 4	Private	16, 18 Oct.	Dry wetland	4	Rectangular	Abundant waste grain	500 m/ 250 m
	9	Adjacent roost 4	Private	11–20 Oct.	Wheat stubble	160	Rectangular	Abundant waste grain	250 m/ 750 m
	10	1 km E roost 5	Private	16–17 Oct.	Bailed wheat field	4	Rectangular	Abundant waste grain	1 km/1 km
	11	Adjacent roost 5	Private	16, 20 Oct.	Partially cut barley	160	Rectangular	Abundant waste grain	1 km/1 km
	12	3 km NW Luseland, Sask.	NR	20 Oct.	Unidentified small grain	760	NR	Waste grain	250 m/NR
	13	88 km W Kiyiu Lake, Sask.	Private	20 Oct.	Wheat stubble	160	Rectangular	Waste grain	250 m/NR
	14	South of Cabri, Sask.	NR	20 Oct.	Unidentified small grain stubble	NR	NR	NR	NR
	15	1 km S roost 6	Private	21 Oct.	Durum wheat strips alternated with plowed fallow	240	Rectangular	Abundant waste grain	500 m/ 3 km
	16	1 km N roost 7	Private	22 Oct.	Wheat stubble	7,250	Rectangular	Abundant waste grain	2 km/ 2–3 km
	17	Adjacent roost 8	Private	23 Oct.	Irrigated alfalfa	64	Round	Alfalfa	350 km/ 1 km
	18	100 m from roost 9	Private	24 Oct.	Picked corn	12	Triangular	Abundant waste corn	Adjacent/ NR
	19	1 km from roost 9	Private	24 Oct.	Picked corn	40	Rectangular	Abundant waste corn	Adjacent/ adjacent
	20	Adjacent roost 10	Private	25 Oct.	Newly sprouted winter wheat	NR	NR	Abundant wheat	NR

Table A2. *Continued.*

Year; color band combination[a]	Site number	Location[b]	Ownership	Dates of use	Cover type	Size (ha)	Shape	Foods	Distance to road/farm
	21	8.5 km S roost 10	Private	25 Oct.	Pasture	40	Rectangular	Abundant sprouted green wheat	250 m/ 500 m
	22	Adjacent roost 11	Private	26 Oct.	Hybrid Sudan cane stubble	50	Rectangular	Numerous insects under cow chips	Adjacent/ NR
	23	3 km S roost 12	Private	27 Oct.	Unharvested milo	46	Rectangular	Abundant milo heads standing in unharvested strip	Adjacent/ NR
	24	4 km from roost 13	Private	28, 29 Oct.	Unharvested milo and millet	20	Rectangular	Abundant unharvested milo heads	Adjacent/ NR
	25	4 km from roost 13	Private	28, 30 Oct.	Newly planted (not yet sprouted) winter wheat	40	Square	Wheat seed just under soil surface	Adjacent/ 250 m
Fall 1982 W-R/W	26	Adjacent roost 17	Private	19, 20 Sept.	Wheat stubble	NR	NR	Wheat	NR
	27	Adjacent roost 17	Private	20–22, 24–27, 30 Sept., 1–11 Oct.	Barley stubble	NR	NR	Barley	NR
	28	NR	NR	21, 24 Sept., 8 Oct.	Stubble	NR	NR	NR	NR
	29	NE roost 17	NR	22 Sept.	Wheat	NR	NR	NR	NR
	30	NR	Private	22 Sept.	Plowed field	NR	NR	NR	NR
	31	2 km N roost 17	NR	23, 24 Sept.	Wheat stubble	NR	NR	NR	NR
	32	W roost 17	NR	23 Sept.	Barley stubble	NR	NR	NR	NR
	33	2 km N roost 17	NR	24 Sept.	Marsh	NR	NR	Probable aquatic vegetation	NR
	34	1 km N roost 17	NR	24 Sept.	NR	NR	NR	NR	NR
	35	1 km E roost 17	NR	25–27, 29–30 Sept.	Barley	NR	NR	Barley	NR
	36	Same as roost 17[d]							
	37	N feeding site 27	NR	8 Oct.	Barley	NR	NR	Barley	NR
	38	Same as roost 18[d]							
	39	E roost 18	NR	9–11 Oct.	Fallow barley	NR	NR	Barley	NR

Table A2. *Continued.*

Year; color band combination[a]	Site number	Location[b]	Ownership	Dates of use	Cover type	Size (ha)	Shape	Foods	Distance to road/farm
W-R	40	6 km E roost 20	Private	12–14 Oct.	Barley stubble	64	Rectangular	Abundant waste barley	600 m/ 3.2 km
	41	6 km E roost 20	Private	12 Oct.	Shallow pond	0.6	Oval	Aquatic plants, invertebrates	600 m/ 3.2 km
	42	4 km E roost 20	Private	14 Oct.	Windrowed, unharvested oats	NR	NR	Abundant scattered oats	NR
	43	NR	NR	14 Oct.	Barley stubble	NR	NR	Barley	NR
	44	NR	NR	14 Oct.	Grain stubble (small)	NR	NR	Grain stubble	NR
	45	Adjacent roost 23	Private	15 Oct.	Grain stubble (small)	NR	NR	Grain stubble	NR
	46	400 m NE roost 23	Private	15 Oct.	Barley stubble	NR	NR	Barley stubble	NR
	47	0.8 km WNW roost 24	Private	16 Oct.	Barley stubble	NR	NR	Barley stubble	50 m/NR
	48	NR	NR	16 Oct.	Oats	NR	NR	Oats	NR
	49	NR	Private	16 Oct.	Barley stubble	NR	NR	Abundant barley stubble	NR
	50	NR	NR	16 Oct.	Stubble	NR	NR	Small grain	NR
	51	NR	NR	16 Oct.	Stubble	NR	NR	Small grain	NR
	52	NR	NR	17 Oct.	Stubble	NR	NR	Small grain	NR
	53	NR	Private	17 Oct.	Scattered, unharvested barley	NR	NR	Abundant barley	NR
	54	NR	NR	17 Oct.	NR	NR	NR	Unknown grain	NR
	55	5 km SE roost 26	Private	18 Oct.	Harvested and plowed barley	NR	NR	Abundant barley	NR
	56	NR	NR	18 Oct.	Barley stubble	NR	NR	Abundant barley	NR
	57	NR	NR	18 Oct.	Barley stubble	NR	NR	Barley	NR
	58	S roost 26	Private	18, 25, 26 Oct.	Wheat stubble	NR	NR	Wheat	NR
	59	NE roost 26	Private	19 Oct.	Small grain	NR	NR	Grain	NR
	60	E roost 26	Private	25, 29 Oct.	Wheat stubble	NR	NR	Wheat	NR
	61	N roost 26	Private	19–27 Oct.	Barley stubble	NR	NR	Barley	NR
	62	Same as roost 26[d]							
	63	NR	NR	28 Oct.	Stubble	NR	NR	NR	NR
	64	NR	NR	29 Oct.	Stubble field	NR	NR	NR	NR
	65	NR	NR	30 Oct.	Wheat stubble	NR	NR	Wheat	NR
	66	Same as roost 30[d]							

Table A2. *Continued.*

Year; color band combination[a]	Site number	Location[b]	Ownership	Dates of use	Cover type	Size (ha)	Shape	Foods	Distance to road/farm
	67	Same as roost 31[d]							
	68	Adjacent to roost 32	Private	1 Nov.	Corn	NR	NR	Corn	NR
	69	Adjacent to roost 32	Private	1 Nov.	Wheat stubble	NR	NR	Wheat	NR
	70	Same as roost 14[d]							
W/R-G	71	400 m S roost 35	Private	15–19, 23, 24 Oct.	Wheat stubble, fallow wheat	60	Rectangular	Abundant waste grain	600 m/ 200 m
	72	1 km S roost 36	Private	17 Oct.	Wheat stubble, fallow wheat	30	Rectangular	Abundant waste grain	600 m/ 1 km
	73	Same as roost 35[d]							
	74	50 m E roost 37	Private	23, 24 Oct.	Native lowland grass, forbs	>1,000	Natural drainage	Insects and tender vegetation	800 m/ 5 km
B/W-R	75	NR	Private	24 Oct.	Wheat stubble, scattered aspen motts	64	Rectangular	Abundant waste grain	200 m/ >3 km
	76	400 m E roost 38	Private	24, 26 Oct.	Wheat stubble	30	Rectangular, depressions throughout	Abundant waste grain	500 m/ 4 km
	77	400 m NW roost 38	Private	25 Oct.	Wheat stubble	64	Rectangular, depressions throughout	Abundant waste grain	600 m/ >5 km
	78	2.5 km W roost 38	Private	26 Oct.	Prob. wheat stubble	64	Rectangular, depressions throughout	Abundant waste grain	2.5 km/ >5 km
	79	5 km NNW roost 38	Private	26 Oct.	Wheat stubble	64	Rectangular,	Abundant waste grain	800 m/ 2.5 km
	80	12 km SW roost 39	Private	27 Oct.	Wheat stubble	64	Rectangular	Abundant waste grain	1 km/ 2.5 km
	81	Same as roost 39[d]							
	82	6 km WSW Timber Lakes, S. Dak.	NR	28 Oct.	NR	NR	NR	NR	NR
	83	30 km SSE roost 41	Private	29 Oct.	Green "July wheat," wheat stubble	8	Long rectangular	Waste grain, green vegetation, possibly grass-hoppers	100 m/ 400 m
	84	110 km SSE roost 41	Private	29 Oct.	Windrow millet	4	Rectangular	Volume windrow	150 m/ 200 m

Table A2. *Continued.*

Year; color band combination[a]	Site number	Location[b]	Ownership	Dates of use	Cover type	Size (ha)	Shape	Foods	Distance to road/farm
								millet, unharvested	
	85	120 km SSE roost 41	Private	29 Oct.	Small grain stubble	10	Rectangular	Abundant waste grain	100 m/ 600 m
	86	5 km NE roost 42	Private	30 Oct.	Millet stubble	1	Rectangular	Waste grain, standing heads	200 m/ 100 m
	87	12 km SE roost 42	Private	30 Oct.	Unharvested corn	4	Rectangular	Exposed corn ears	150 m/ 600 m
	88	10 km N roost 43	Private	31 Oct.–1 Nov.	Corn stubble	NR	NR	Waste corn	NR
	89	8 km N roost 43	Private	31 Oct.	Water-filled windmill depression and adjacent native pasture	NR	NR	Roots, snails, frogs, spiders, insects	NR
	90	5 km N roost 43	NR	31 Oct.	Upland pasture, short over-grazed grass	NR	NR	Grasshoppers, spiders, crickets	NR
Spring 1983 W-R	91	0.5 km E roost 77	Private	12–16 Apr.	Milo stubble, green winter wheat 20 cm tall	32	Rectangular	Abundant milo seed, corn and beetles associated with cow chips	200 m/ 500 m
	92	Same as roost 78[d]							
	93	35 km ESE roost 79	Private	17 Apr.	Slough in creek running through field	0.2	Long, narrow	Unknown winter wheat	250 m/NR
	94	35 km ESE roost 79	Private	18 Apr.	Milo stubble	30	Rectangular	Milo	250 m/NR
	95	8 km NNW roost 79	Private	18 Apr.	Milo stubble, 35 cm tall	40	Rectangular	Milo	300 m/NR
	96	1.6 km S roost 81	Private	19, 20 Apr.	Wheat stubble, 35–40 cm tall	40	Square	Wheat	350 m/NR
	97	0–2 km from roost 82	Private	20–30 Apr.	Wheat stubble	250	Rectangular	Wheat	800 m/NR
	98	300 m SE roost 82	Private	20–30 Apr.	Marsh where creek delta entered lake	0.4	Triangular	Invertebrates	1 km/NR

Table A2. *Continued.*

Year; color band combination[a]	Site number	Location[b]	Ownership	Dates of use	Cover type	Size (ha)	Shape	Foods	Distance to road/farm
	99	Adjacent roost 83	Private	30 Apr.–1 May	Wheat stubble	50	Square	Wheat	800 m/NR

[a]Colors: white, red, green, blue, yellow. Combination order: upper/lower left leg-upper/lower right leg.
[b]See Table A1 for roost site locations.
[c]NR = not recorded.
[d]See corresponding roost in Table A1 for data.

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Howe, Marshall A. 1989. **Migration of Radio-marked Whooping Cranes from the Aransas–Wood Buffalo Population: Patterns of Habitat Use, Behavior, and Survival.** U.S. Fish Wildl. Serv., *Fish Wildl. Tech. Rep.* 21. 33 pp.

Use of migration stopovers by radio-tracked whooping cranes (*Grus americana*) was studied in fall 1981–83 and spring 1983–84. Information on habitat use, time-activity budgets, and hazards encountered is presented for a sample of 27 individuals, including 9 radio-marked birds. Survival rate is calculated for radio-marked birds and compared with estimates for birds not radio-marked. Distribution patterns of birds for which complete stopover information is available are contrasted with distributions derived from opportunistic observations.

Key words: Whooping crane, *Grus americana*, radiotelemetry, migration, habitat use, staging area, behavior, time-activity budget, survivorship, mortality.

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